99

TAXONOMY AND ECOLOGY OF SOUTH AFRICAN REEF CORALS

by Bernhard Riegl

Thesis Presented for the Degree of

DOCTOR OF PHILOSOPHY

in the Department of Zoology

UNIVERSITY OF CAPE TOWN

August, 1993

TAXONOMY AND ECOLOGY OF SOUTH AFRICAN REEF CORALS

Bernhard Riegl
Zoology Department, University of Cape Town, Rondebosch 7700
15. August 1993

Short abstract

This thesis provides a complete taxonomic review of South African hermatypic Scleractinian reef corals, a description of coral communities on northern Natal coral reefs, experiments isolating the influence of the most important abiotic factors forcing these communities and finally management suggestions for the marine reserves within which these reefs are situated, based on the results of the ecological investigation.

The taxonomic part reviews the entire hermatypic scleractinian coral fauna of South Africa and Southern Mozambique, including also material from the Atoll Bassas da India in the Mozambique channel.

The study of coral communities on Northern Natal coral reefs revealed major differences in the nature of the reefs and the community structure of the reef corals from typical coral reefs in the Indo-Pacific. The study lead to the assumption that wave-action and sedimentation are the most important abiotic factors influencing these coral communities.

These hypotheses were experimentally tested in the field and in the laboratory, using indicator species for specific community types, as identified in the community study.

Testing fragment survival of the hard coral Acropora austera confirmed the assumption that wave action is an important factor shaping coral communities by only allowing this species to dominate in depths greater than 18m.

Four hard- and five soft coral species were used to quantify the effects of sedimentation on the coral communities. It was demonstrated that long-term sedimentation had greater influence on soft corals than on hard corals, leading to tissue necroses and local bleaching. These experiments confirmed the assumption that sedimentation is a major forcing factor on South African coral communities.

The final part of thesis provides management options for the St. Lucia and Maputaland Marine Reserves focussing on conservation of the coral communities. The findings obtained in the ecological investigation allowed to identify which activities in the reserves have to be controlled in order to minimize damage to the coral communities by park visitors.

Acknowledgements

Although a thesis is per definition the work of only one person, there are always a great number of people without whose contribution this work would never have been possible.

First of all, I would like to thank my wife Andrea for her patience and for putting up with the long time we were separated.

I am greatly indebted to my three supervisors, Prof. George Branch (UCT), Dr. Peter Cook (UCT) and Dr. Michael Schleyer (ORI). Without their help this thesis would have never come together or it would not have come so far. From each of them I learned a great lot. Dr. Martin Brooks and Dr. Orty Bourquin (Natal Parks Board) helped me to obtain permits to work in the St. Lucia and Maputaland Marine Reserves and provided me with a vehicle for use during the project. Prof. Antonio de Freitas, Dr. Michael Schleyer and Mr. Rudy van der Elst (ORI) provided me with office space and financial support at the Oceanographic Research Institute in Durban, which was crucial for the success of my work. Mr. Tim Kay (ORI) was an excellent skipper and cook during our field trips. Mr. John Ballard (ORI and Sea World, Durban) helped me to construct and maintain my laboratory experiments and helped me with the water chemistry measurements. He never moaned when I broke one of his aquaria or stole one of his display animals for my experiments. Mr. Bill Howles and Mr. Ed Smith of Sodwana Bay National Park always fully supported me while I was based in Sodwana and made my life much easier and very enjoyable. Dr. Willem Prinsloo provided me with his friendship, house, boat and bakkie whenever I needed his help. Dr. Carden Wallace of the Queensland Museum helped me with Acropora taxonomy and Dr. Hudi Benayahu of Tel Aviv University gave me a lot of good ideas and time for the discussion of problems during his visits to South Africa. Prof. John Field and Rodrigo Bustamante (UCT) helped me with their statistical know-how; Rodrigo was very patient and always present and pleasent, without his help the stats in this thesis would probably be horrible! Prof. Rolf Behrens, then of the SA embassy in Vienna, helped me with visas and scholarships.

Financial support was provided by the Foundation for Research Development, the Department of National Education, the Endangered Wildlife Trust, the SA Association for Marine Biological Research, the University of Cape Town, the South African Underwater Union and the Natal Underwater Union.

But most of all I have to thank my friends who never failed to support me. I can't mention all, but special thanks are due to Willem and Sharon Prinsloo in Durban and Deon, Justin & the boys in Cape Town. You're all a splendid lot!

Index

GENERAL ABSTRACT

This thesis provides an overview of the reef-coral fauna of South East Africa and a description of patterns and processes underlying coral communities in Maputaland, Northern Natal, South Africa.

The taxonomy of the entire hermatypic scleractinian hard coral fauna of South Africa and Southern Mozambique, including also material from the Atoll Bassas da India in the Mozambique channel, was reviewed. Four new species in the genus Acropora are described.

A detailed study of Maputaland coral communities revealed major differences in the geomorphology of the reefs and coral community structure from typical coral reefs in the tropical Indo-Pacific. The community study lead to the hypotheses that sedimentation and wave-action are the most important abiotic factors shaping the communities. These hypotheses were tested in both field- and laboratory experiments using indicator species identified in the community study for specific community types.

The hard coral Acropora austera was used to test the assumption that wave-action is an important factor shaping coral communities by restricting dominance of this species to depths greater than 18m. The tested hypothesis was that wave action caused breakage of the colonies and thus generated fragments, which could be used for asexual reproduction. This in turn would facilitate dominance by creating daughter colonies consisting of reattached fragments in suitable habitats. The survival of fragments was tested in different depths and on different substrata. It was demonstrated that fragment survival, colony size and total numbers of colonies were significantly correlated with depth, and therefore decreasing wave-action.

were significantly correlated with depth, and therefore decreasing wave-action.

Four hard- and five soft-coral species were used in laboratory studies to quantify the effects of sedimentation on the coral communities. It was demonstrated that long-term sedimentation had less influence on hard-corals than on soft-corals, which suffered a higher incidence of tissue necroses and local bleaching. Short-term sedimentation on the same species of hard- and soft-corals provoked similar physiological reactions, characterized by decreased production and respiration. The proportion of respiration in production increased, however. The effects of sedimentation on the energy balance of these corals was modelled from the data obtained during the experiment. Sedimentation caused the P/R ratios of most species to drop below unity, signalling that the loss of photosynthetic production due to coverage by sediment significantly interfered with the coral's energy balance. These experiments proved that sedimentation is a major factor shaping South African coral communities.

The final part of the thesis provides management options for the St. Lucia and Maputaland Marine Reserves focussing on conservation of the coral communities. The empirical findings of the ecological investigation allowed to identify which activities in the reserves have to be controlled in order to minimize damage to the coral communities by park visitors.

GENERAL INRODUCTION

Coral communities, as an important part of one of the world's most diverse ecosystems, provide an ideal opportunity to learn about the functioning of complex biological systems. While tropical coral reefs are well studied, much fewer studies exist on subtropical coral reefs or coral communities (Crossland, 1988). Also, coral studies of any type on the African continent, and especially studies on reef-corals, are few and far between (Wijsman-Best et al., 1980; Boshoff, 1981; Hamilton & Brakel, 1984; van Ofwegen & Benayahu, 1992).

Reef-corals are not only key organisms for ecosystem diversity in the tropics due to their reef-building and thus habitat creating activity, a fact which merits attention in its own right, but coral ecosystems also attract large numbers of tourists and have thus become important economic factors.

On the African continent, coral reefs are only found on the East Coast. On the West Coast they are missing due to cold water upwelling off South-West and West Africa, and the influence of the large Central African rivers (Schuhmacher, 1991). The southernmost reef-coral communities in Africa are found on the Maputaland coast in northern Natal at 27°50' South. This puts them at the South Western extremity of the Indo-Pacific reef-coral fauna and also makes them one of the southernmost reef-coral communities in the world.

The Maputaland coral reefs are situated within two Marine Reserves, the St. Lucia and Maputaland Marine Reserves. They are one of South Africa's major tourist attractions and have over the

last five years witnessed a rapid increase in the number of visitors. This has prompted concern on the side of conservation authorities that degradation of the coral communities might be imminent and the need for management options based on a sound understanding of the area's fauna and ecology was realized.
It is the aim of this thesis to provide sufficient information about the fauna and the ecology of these coral communities to make a contribution as well to science as to nature conservation by offering the first detailed description of the area's fauna and the patterns and processes underlying South African coral communities.

Part I of the thesis is a detailed taxonomic revision of the entire hermatypic hard coral fauna of South Africa. It also takes material from southern Mozambique and the Atoll Bassas da India in the Mozambique channel into account. This allows to observe gradients in species richness with increasing latitude. The hard coral fauna of the area was previously almost unknown, as the few existing publications were either based on incomplete collections (Wijsman-Best et al., 1980) or full of misidentifications and taxonomic errors (Boshoff, 1981; Ramsey & Mason, 1990).
Part II of the thesis describes the coral communities in relation to substratum and environmental factors. This is the part where the hypotheses concerning the functioning of the system will be developed.
Part III will use indicator species for distinctive communities as described by the community study to test the hypotheses formulated in Part II experimentally.

Part IV will use all the information obtained in the previous parts to assess the status of the South African coral communities, to identify areas susceptible to damage and also to identify which forms of use are most likely to damage the coral communities. Management options based on these findings will be provided.

P A R T I

The fauna: taxonomy

In this first part of the thesis I will give an overview over the sofar almost unknown hard coral fauna of South Africa and southern Mozambique. Previous records are very unreliable due to inaccuracies and numerous taxonomic errors. This made a complete revision of the fauna neccessary.

THE HERMATYPIC CORAL FAUNA OF SOUTHERN AFRICA. A REVISION WITH IDENTIFICATION KEYS

Abstract

This chapter gives an overview over the hermatypic scleractinian coral fauna known to occur in South Africa. Exept the genus Acropora and the families Faviidae and Poritidae, which are treated in seperate chapters, all other species are treated in detail. Short notes are added on species occurring in Mozambique but not in South Africa. Additionally, an overall identification key, leading to genera is provided. Where neccessary, further keys to the species are added. The paper is based primarily on extensive collections of corals from the reef system in Maputaland and the Natal coast. Material from Inhaca Island and the Mozambique coast was also taken into account. The South African hermatypic coral fauna comprises 90 species, most of which are recorded here for the first time. The South African coral fauna was poorer than the Mozambiquan. The fauna becomes increasingly poorer as one moves south down the East Coast of Southern Africa, reflecting the fact, that the reef systems are at the south-westerly extremity of the Indo-Pacific fauna.

Introduction

The eastern shores of Africa represent the western boundary of the world's largest biogeographical province, the Indo-Pacific. In recent years much effort has been put into detecting patterns in the distribution of coral diversity and species richness across this area (Sheppard, 1987; Sheppard & Sheppard, 1991). The general picture is, that the highest diversity exists in the centre of the province, in South-East Asia, and decreases towards the edges. Irregularities have been detected in the North-East African and Arabian region. There, a distinct and very diverse sub-region has been detected (Sheppard, 1987; Sheppard & Sheppard, 1991; Jokiel & Martinelli, 1992). Three other subregions were described by Sheppard & Sheppard (1991), one in the South-West Indian Ocean, including the South East African coast. While the Red Sea and Western Australia have received considerable attention in terms of coral systematics (Sheer & Pillai, 1983; Head, 1984; Veron & Marsh, 1988; Sheppard & Sheppard, 1991) the same, however, does not apply to the tropical and subtropical East African coast (Wijsman-Best et.al. 1980; Boshoff, 1981), with the southernmost corner, South Africa, having been almost completely ignored. Records that do exist, are unreliable and largely based on misidentifications (Boshoff, 1981; Ramsey & Mason, 1990) and a big piece in the puzzle of biogeographic regions is thus still missing. As long as this has not been filled in, big gaps remain in our understanding of coral distribution and we cannot appreciate whether South East Africa is really exceptionally rich in coral species, as could be postulated according to recent bio-

geographical hypotheses (Jokiel & Martinelli, 1992).

This study provides a list of all hermatypic coral species found in South Africa. Notes on the species from the subtropical Mozambiquan coast are also included, although the list for this area is possibly not complete. Thus it will be possible to appreciate the species richness of a sofar largely ignored region which, as the southern extreme of hermatypic coral occurrence in the Western Indian Ocean, is of great biogeographical significance.

This paper provides not only a listing of species but also identification keys, in order to make it a useful tool in the field, away from the desk and theory.

Material and methods

Corals were collected on all major reef sites south of the tropic of Capricorn. Principal collecting sites were in the Maputaland reef system in northern Natal, South Africa. Material from Mozambique was collected mainly at Inhaca Island off Maputo and on selected sites along the coast (Fig.1).

This paper is based on observations derived from a collection of several hundred specimens located with the Oceanographic Research Institute in Durban, the South African Museum in Cape Town, the Zoological Museum of Tel Aviv University and material collected by the author. It has been complemented by field observations, which are indispensible in order to allow statements concerning morphological variations and the actual frequency of the species in their natural environment.

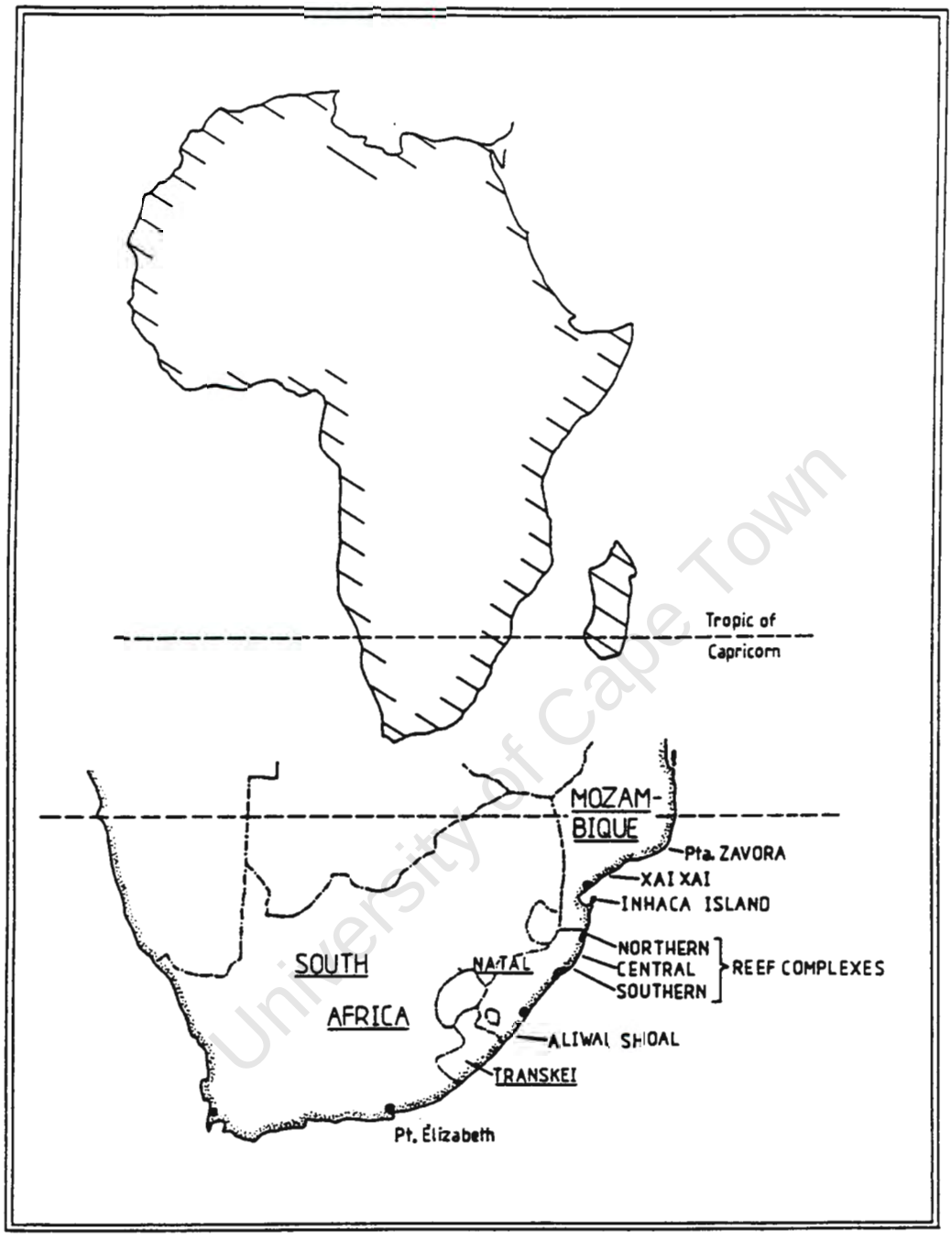
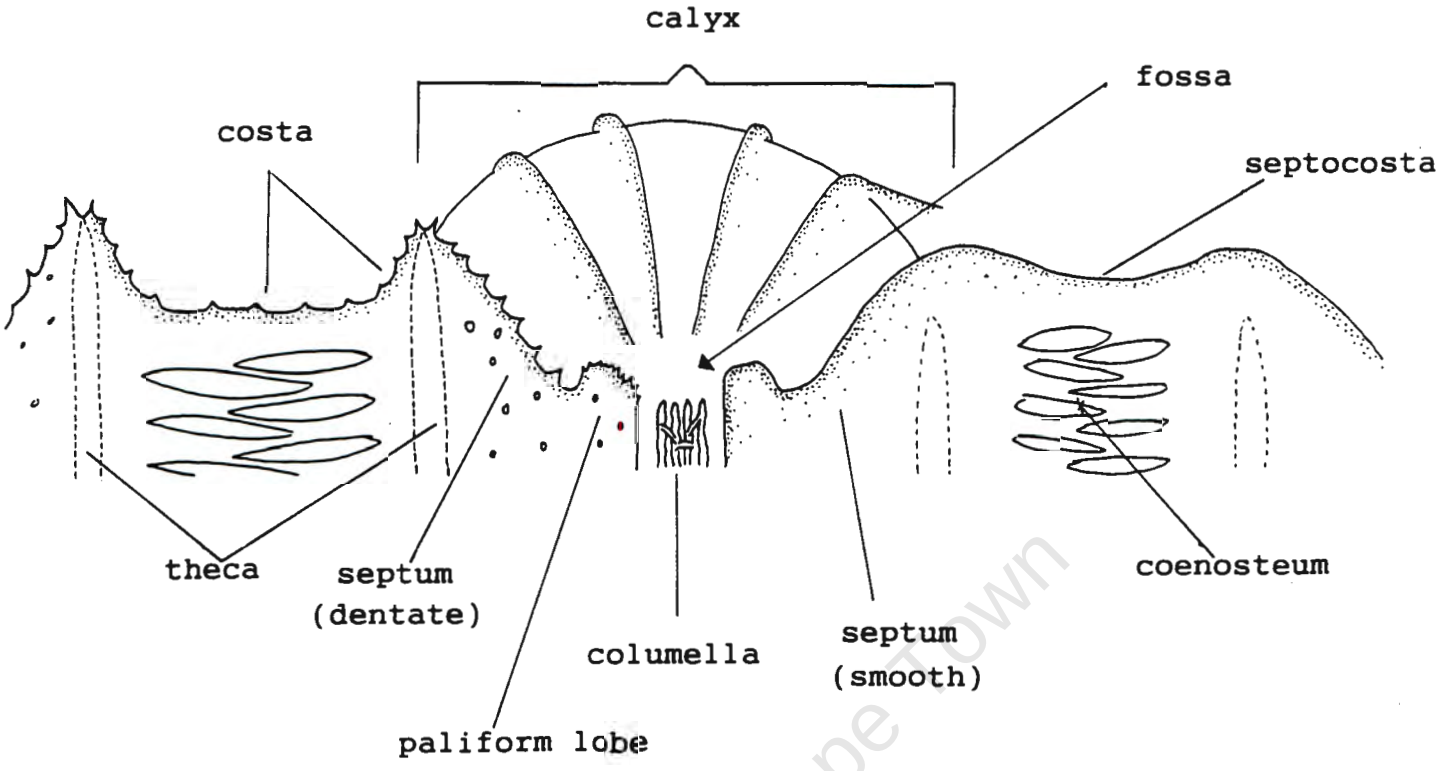


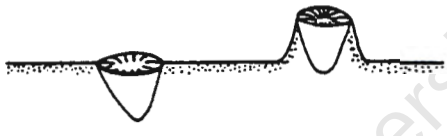
Fig. 1: Overview of South East Africa showing the overall geographical setting of sample locations along the South African and Mozambiquan coast.

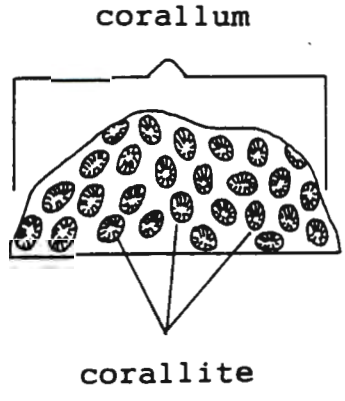
Taxonomic note

Corals are among the most plastic animals in terms of their growth form, which may vary widely. Correct identification can rarely be based on single specimens, even more so if nothing is known about the ecological conditions in which they grew. The growth form and the shape of the corallum alone may in some instances not be very good diagnostic features, as they may vary with age and environmental conditions. They are, however, the most apparent characters of any specimen and growth form types are, despite all variability, still characteristic for most species or genera, at least within certain limits. Therefore, the present keys use growth form as one of the first and most important differentiating tools. This approach was possible as growth forms were found to be remarkably uniform on South African reefs. This is a result of the very uniform environmental conditions reigning around these coral communities (see Part II, Chapter 1). As these keys are based on a large collection (several hundred specimens) and extensive field observations they take into account most of the common growth variations found in South Africa. Outside the area specified (see Fig. 1), even where the same species can be found, these keys may in certain instances be only of limited value, because, due to different environmental conditions, the growth forms of the corals may vary more widely than given room for in the present keys. In this case (and in the case of South African specimens with aberrant growth forms), the monographs on generic or familial level will have to be consulted (see Part I, chapters 2, 5 & 6).

Figure 2, Part 1







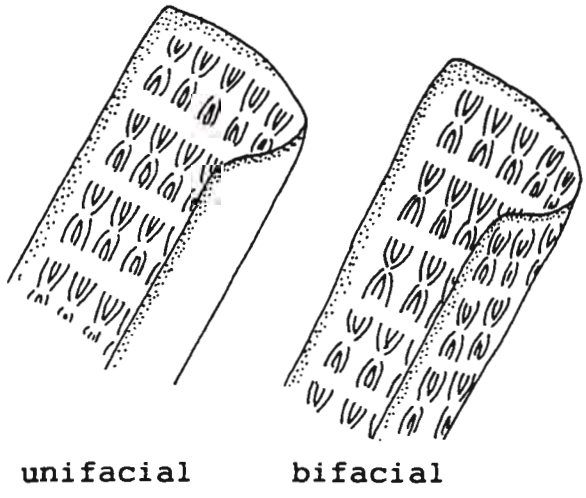


Figure 2, Part 2

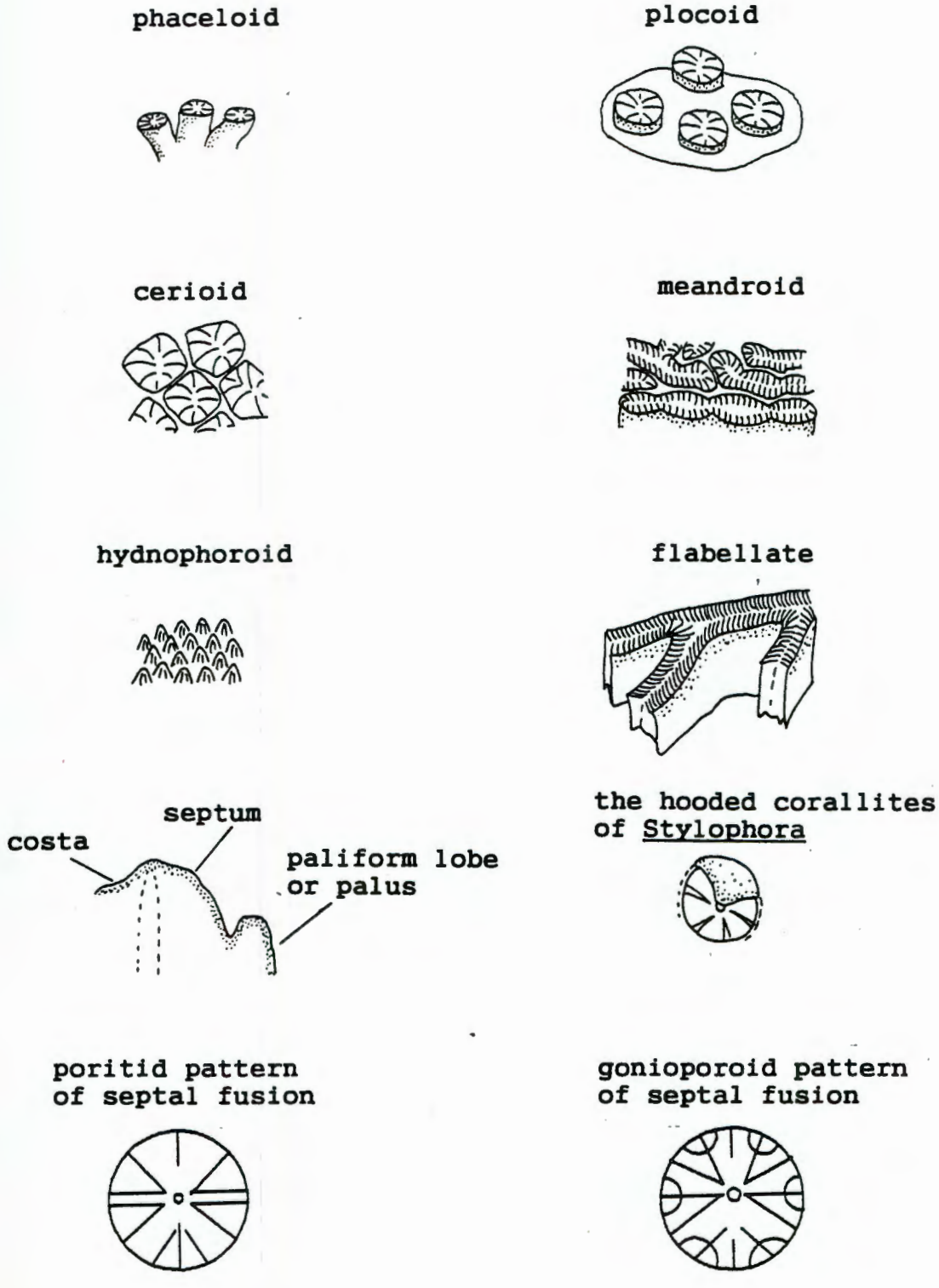


Fig. 2: Explanation of terms used in the identification key.

KEY ONE

1 Corallum attached.....2

1* Corallum unattached.....Fungiidae (p.44)

2(1) Corallum colonial.....3

2* Corallum solitary.....Scolymia (p.63)

3(1) Corallum branching.....4

3* Corallum not branching, but may be massive, encrusting or platelike.....8

4(3) Branches ending always in a single apical corallite.....most species of Acropora (p.29)

4* Branches never ending in a single apical corallite.....5

5(4*) Branches mostly laterally compressed, thick and blunt, often wedge-shaped.....6

5* Branches mostly round or almost round, tip rounded to pointed.....7

6(5) Coenosteum covered with wart-like protrusions, corallites without septa.....Pocillopora (p.19)

6* Coenosteum not covered with warty protrusions, corallites well exsert, with septa.....Acropora palifera

7(5*) Corallites hooded, branches blunt.....Stylophora (p.19)

7* Corallites hooded or surrounded by a ring, branches thin and pointed.....Seriatopora (p.17)

8(3) Corallum submassive to massive; colonies flat, cushionlike hemispherical to spherical.....24

8* Corallum different, usually encrusting or platelike.....9

9(8*) Corallum encrusting or platelike.....10

9* Corallum encrusting to massive, surface smooth, ridged or hillocky.....23

10(9) Corallum encrusting, sometimes with platelike edges or short branches.....19

10* Corallum platelike; flat growing, funnel-shaped vase-shaped or warped.....11

11(10*) Corallum a flat growing plate, only the centre slightly depressed, unifacial, corallites continuous.....12

11* Corallum vase-shaped, funnel-shaped or warped.13

12(11) Corallites fused to form long parallel valleys (Plate 13b).....Pachyseris (p.42)

12* Corallites not forming valleys but with well developed costae connecting the centres.....Leptoseris (p.39)

13(11*) Corallum a vase or funnel shaped plate, large (up to 2m diameter), bifacial, apical corallite visible on growing edge.....Acropora clathrata (p.30)

13* Corallum unifacial.....14

14(13*) Corallum regular and funnel-shaped.....15

14* Corallum leaf-like and contorted.....18

15(14) Corallites exsert.....16

15* Corallites immersed.....17

16(15) Vase or funnel-shaped, sometimes warped, large (up to 2m diameter), growing edge smooth, corallites exser, around 5mm diameter, costae not continuous between corallites.. .....Turbinaria (p.68)

17(15*) Funnel-shaped, small (around 30cm diameter), corallites immersed, about 10mm diameter, costae continuous between corallites.....Podabacia (p.53)

18(14*) Corallum thin, unifacial, contorted, large, corallites well exsert and spiky, dentations large and simple, never forming branches or short columns.....Echinophyllia (p.55)

18* Corallum similar, also with spiky corallites, but sometimes forming short branches or columns.... .....Echinopora (p.65)

19(10) Corallum encrusting and thin, edges may be plate-like, then bifacial, corallites tiny (-2mm), always immersed, coenosteum often decorated with small humps.....Montipora (p.22)

19* Corallum encrusting and thick or with branches....20

20(19*) encrusting to submassive with protruding short branches or very irregular tubular corallites with short corallites grouped around them in form of a rosette.....some species of Acropora

20* Encrusting without exsert corallites.....21

21(20*) Encrusting with shallow corallites with continuous costae.....23

21* Encrusting with distinct, deep corallites, costae not continuous.....22

22(21*) Small to medium sized (2-5mm diameter) round corallites with typical poritid pattern of septal fusion (see Fig. 2).....Poritidae (p.30)

22* Medium to large corallites (>5mm diameter), septa never fused in the poritid pattern.....29

23(21) Encrusting to massive, surface hillocky, corallites plocoid, small (about 3mm), septal pattern resembling a flower (Plate 8a)..... Psammocora (p.31)

23* Encrusting to massive, surface smooth or with ridges, corallites plocoid, medium to large (3-5mm), costae continuous.....Pavona (p.37)

24(8) Massive growth form, skeleton dense and robust..25

24* Massive growth form, skeleton light, spongy and very porous.....Alveopora (p.31)

25(24) Corallites with septa.....26

25* Corallites without or with only very weak septa... .....Astraeopora (p.30)

26(25) Each corallite associated with a small, styliform pillar (see Plate 1a).....Stylocoeniella (p.15)

26* Styliform pillar not present.....27

27(26) Massive, corallites of various sizes, 2 shapes, septa never fused in gonioporoid or poritid pattern.....29

27* Massive, corallites small to medium (up to 5mm), never exsert, mostly round, septa distinctively fused in either gonioporoid or poritid pattern..28

28(27*) Corallites medium (around 5mm), gonioporoid pattern of septal fusion (see Fig.2.).....Goniopora (p.31)

28* Corallites small (around 2-4mm), poritid pattern of septal fusion (see Fig. 2).....Porites (p.31)

29(22*, 27) Corallites plocoid.....30

29* Corallites other than plocoid.....40

30(29*) Corallites fully fused with compact and continuous coenosteum.....32

30* Corallites only partly fused, coenosteum with clearly visible gaps. Corallites very uniform in size, round, regular septation, fused in a bead-like manner forming rows, leaving large pores, septa smooth and regular (Plate 21a).....Blastomussa (p.57)

31(30) Fossa deeper than surrounding coenosteum (i.e. immersed, or exsert, but partly immersed).....34

31* Fossa does not reach level of surrounding coenosteum (i.e. corallite is not immersed at all) but exsert by more than 1 corallite diameter, 12 septa, long, vertical spines on septa,spiky appearance .....Galaxea (p.53)

32(31) Small, plocoid corallites, wall never well developed, fully immersed or hardly exsert with clear costae thazt are continuous, massive to submassive, also encrusting.....23

32* Plocoid corallites, wall well developed.....33

33(32*) Small corallites, never wider than 5mm.....34

33* Large corallites, always wider than 5mm.....37

34(33) Always 24 Septa in two clearly distinguished size classes.....Cyphastrea (p.65)

34* Different number of septa, differentiated into less

or more than 2 size classes.....35

35(34*) Corallites round and regular, septa in three cycles, no true palis, costae present.....Montastrea (p.66)

35* Either no costae, or true palis present..... 36

36(35*) Corallum very similar to Montastrea, corallites with costae, but true palis present.....Plesiastrea (p.66)

36* Costae never present, well developed intercalicular groove, plocoid to subcerioid, encrusting to massive.....Leptastrea (p.65)

37(33) Large (around 10-20mm), mostly well developed corallites, round to polygonal, dentations on septa mostly conspicuous, less than 40 septa.....Favia (p.65)

37* Large corallites (10-15mm), rarely round but usually oblong, in S.A. mostly subcerioid but in Mozambique plocoid, more than 40 septa with short dentations.....Horastrea (p.35)

38(29*) Corallites cerioid.....39

38* Corallites other than cerioid.....43

39(38) Fossa very deep, septa smooth, never paliform lobes.....40

39* Fossa shallower, septa with dentations and paliform lobes.....42

40(39) Columella present, corallites often very irregular in outline.....41

40* Columella absent, corallites of regular size and shape.....Coeloseris (p.40)

41(40) About 50 septa with smooth or granular margins,

stout columella.....Gardineroseris (p.40)

41* About 30 septa, margins with small dentate spines, elongate columella.....Anomastrea (p.33)

42(39*) Corallites very regular in size and shape (usually <7mm), rounded, true palis always developed..Goniastrea (p.65)

42* Corallites often very irregular in size (7-30mm) and outline, paliform lobes not always present..Favites (p.65)

43(38) Corallites hydnophoroid.(Fig. 2).....Hydnophora (p.63)

43* Corallites else than hydnophoroid.....44

44(43*) Corallum meandroid, or tending towards a meandroid condition, corallites <25mm wide.....45

44* Corallum different, not meandroid, corallites very large (>30mm) and with spiky septa.....49

45(44) Corallum entirely meandroid.....47

45* Corallum sub-meandroid or plocoid with individual corallites forming short series.....46

46(45*) Walls well defined, small to medium sized corallites, true palis present.....Goniastrea (p.65)

46* Walls wide but low, fossae of varying depth, costae continuous between corallites.....Coscinaraea (p.33)

47(45) Meander width around 5mm.....48

47* Meander width much greater than 5mm (around 15-20mm), walls acute and perforate, septocostae well exsert with trabecular linkage, columella spongy, valley length very irregular.....Oulophyllia (p.65)

48(47) Walls acute, septocostae well exsert, septa with large dentations, spongy columellae, valley

lengths very variable, irregular appearance..Platygyra (p.65)

48* Septa with fine dentations, septocostae not acute, but horizontal, columella platelike, very regular appearance .....Leptoria (p.66)

49(44*) Centre of the colony meandroid, becoming flabello-meandroid on the edges, whole colony fused and compact.....Symphyllia (p.61)

49* Colonies phaceloid to flabellate; centres may be linked to form series but laterally almost always free; most corallites are only loosely connected..Lobophyllia (p.61)

Phylum **Coelenterata** Frey & Leuckart, 1847

Class **Anthozoa** Ehrenberg, 1834

Order **Scleractinia** Bourne, 1900

Family **Astrocoeniidae** Koby, 1890

This is a small family consisting only of a single extant genus. Although in Australia it appears to be very conspicuous on high latitude reefs (Veron, 1986), this is not the case in Southern Africa.

Genus **Stylocoeniella** Yabe & Sugiyama, 1935

This generally uncommon genus has so far only been recorded from Mozambique.

Stylocoeniella guentheri Basset-Smith, 1890 (Plate 1a)

Stylocoenilla guentheri Basset-Smith; Veron & Pichon, 1976; Veron, 1986; Sheppard & Sheppard (1991).

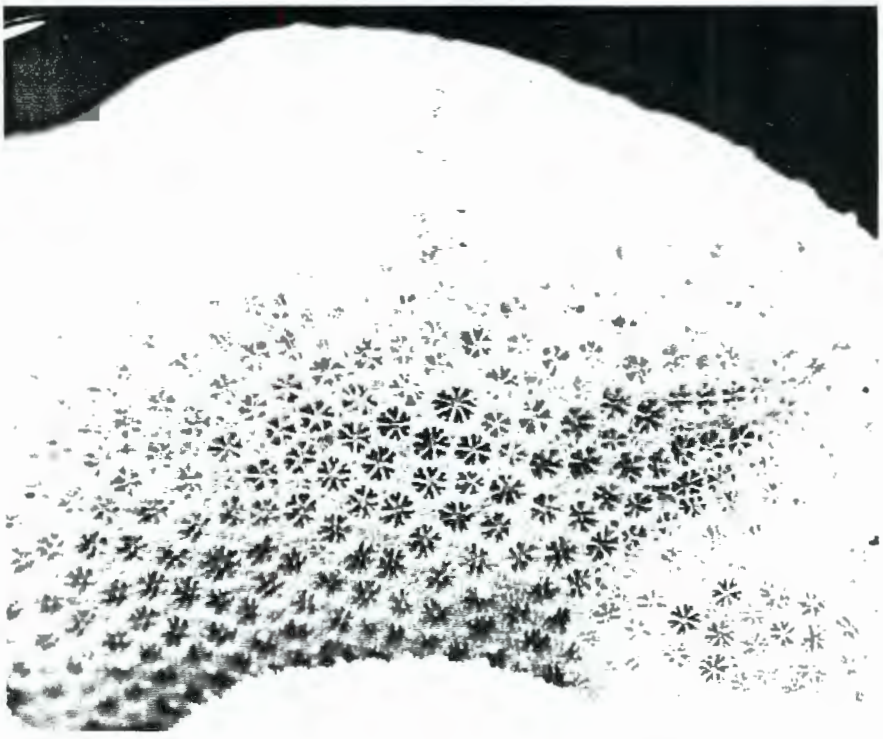


Plate 1a: Stylocoeniella guentheri, Inhaca Island, x5.

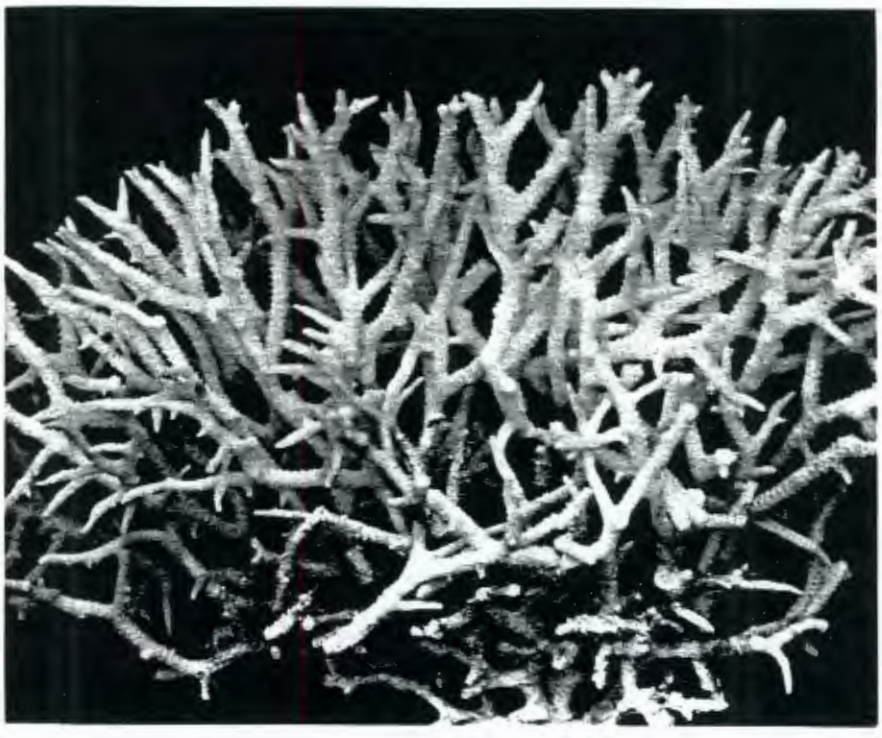


Plate 1b: Seriatopora hystrix, Inhaca Island, x1.

Only one record from Inhaca Island. Colonies are solid and round colonies. Associated with each corallite is a little, styliform pillar, which makes this genus easily recognizable. Corallites are small with two septal cycles.

Family Pocilloporidae Gray, 1842

This family is widespread all across the Indo-Pacific and some of the species are abundant on almost every reef-system within this area. Five species occur in our area.

Genus Seriatopora Lamarck, 1816

It is not certain whether this genus occurs at all in South Africa, as present records are dubious. It is however frequently found from Inhaca Island northwards. In this genus calices are typically aligned in rows, which provides a good clue in the field to distinguish it from Stylophora.

Seriatopora caliendrum Ehrenberg

Seriatopora caliendrum Ehrenberg; Veron & Pichon (1976); Scheer & Pillai (1983); Sheppard & Sheppard (1991).

This species is characterized by long and narrow, anastomosing branches. The corallites are typically hooded or surrounded by a raised ring. Branch end are blunt. It has been recorded from South Africa (Central Reef Complex, Northern Natal) and Mozambique (Bazaruto Archipelago).

Seriatopora hystrix Dana, 1846 (Plate 1b)

Seriatopora hystrix Dana; Veron & Pichon (1978); Scheer & Pillai (1983); Sheppard & Sheppard (1991).

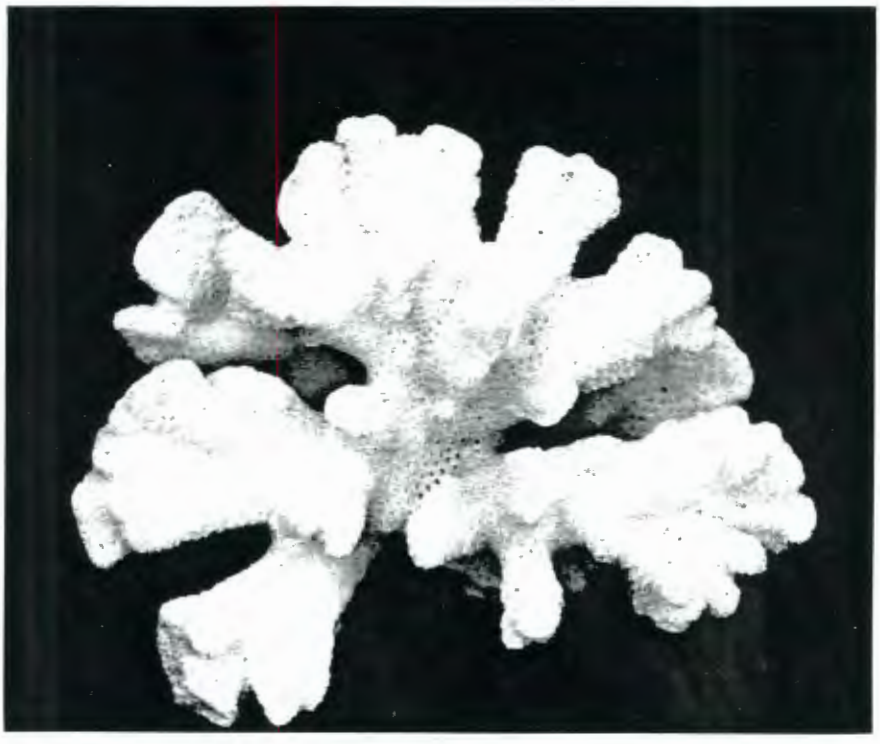


Plate 2a: Stylophora pistillata, 9-Mile Reef, South Africa, x1

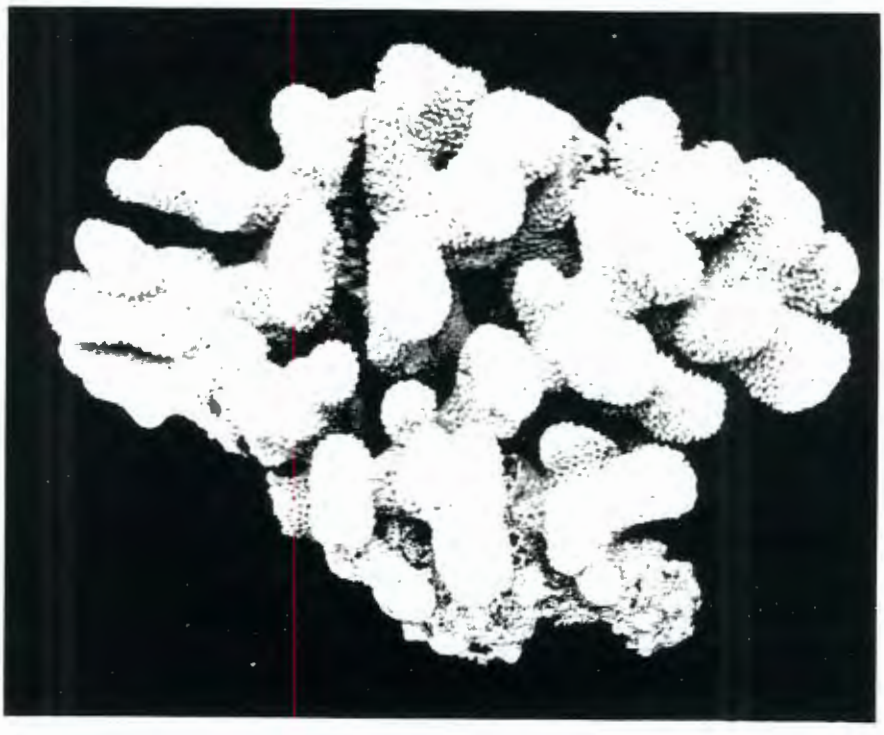


Plate 2b: Stylophora pistillata, 2-Mile Reef, South Africa, x0.5

The branches are thinner and much more pointed than in the previous species; they also anastomose. Colony shape is usually neatly round. The branches are very fragile. This species occurs from Mozambique (Inhaca Island) northwards.

Genus **Stylophora** Schweigger, 1819

This is also one of the very common genera, especially in the Indian Ocean. The exact number of species in this genus is matter of ongoing debate, as there seems to be a high degree of local endemism (Sheppard & Sheppard, 1991).

Stylophora pistillata Esper, 1797 (Plates 2 a&b)

Stylophora pistillata Esper; Veron & Pichon (1976); Sheer & Pillai (1983); Sheppard & Sheppard (1991).

This is one of the most common species on tropical coral reefs in the Indian Ocean. In the subtropics however it is not so common. In South Africa it typically grows in very small colonies with either narrow, round or flattened, paddleshaped branches. It occurs from the Eastern Cape Province (Port Elizabeth) north.

Genus **Pocillopora** Lamarck, 1816

Two species (P. verrucosa and P. damicornis) occur with certainty in our area, the occurance of a third is dubious. They are common on all reefs.

Key:

1 Branches blunt and markedly bigger than verrucae.....2

1* Branches often pointed and intergrade with verrucae, which are large and often develop into branches.....P.damicornis

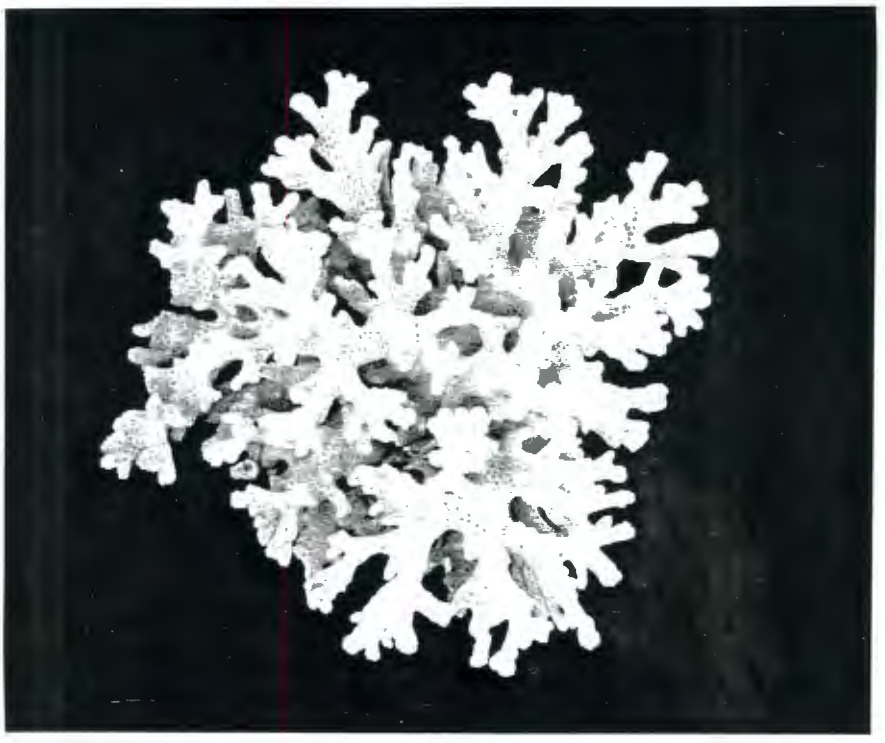


Plate 3a: Pocillopora damicornis, Inhaca Island, Mozambique, x0.3

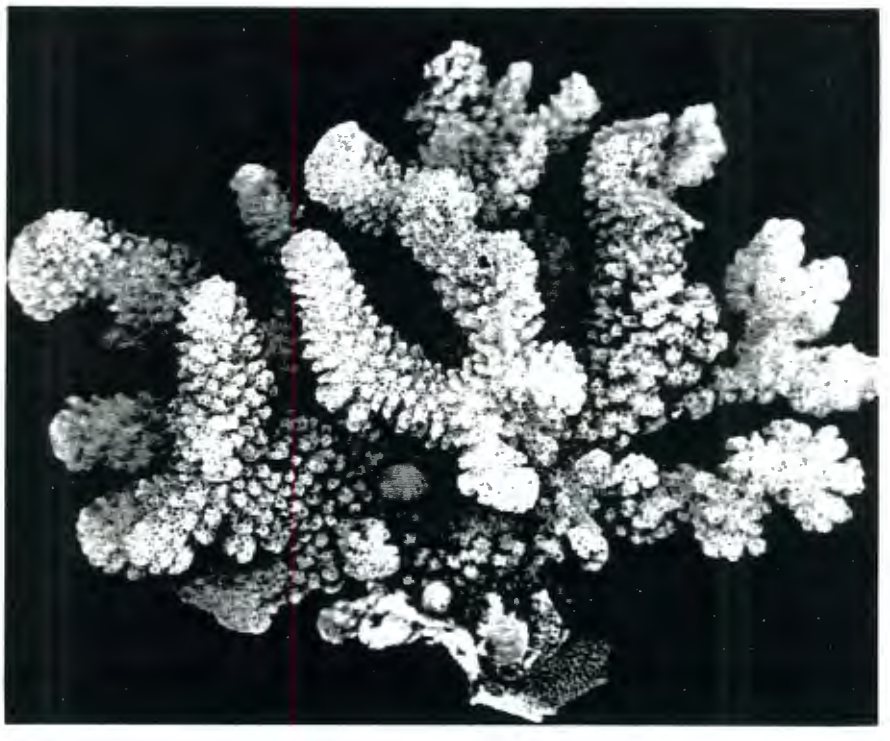


Plate 3b: Pocillopora verrucosa, 2-Mile Reef, South Africa, x0.3

2(1) Branches wide and stout, growing upwards with big, irregular verrucae.....P.verrucosa

2* Branches vary from narrow and round to wide and paddle-like, small verrucae with rough coenosteum.....P. eydouxi

Pocillopora damicornis (Linnaeus, 1758); (Plate 3a)

Pocillopora damicornis (L.); Veron & Pichon (1976); Scheer & Pillai (1983); Sheppard & Sheppard (1991).

Colonies are small with slender branches. The verrucae, which are typical for this genus, are irregular and intergrade with the branches. It is sometimes not possible to distinguish between verrucae and incipient branchlets. This species is only known to occur from Inhaca Island, Mozambique, northwards. It has not yet been observed in South Africa.

Pocillopora verrucosa (Ellis & Solander, 1786) (Plate 3b)

Pocillopora verrucosa (Ell.& Sol.); Veron & Pichon (1976); Scheer & Pillai (1983); Sheppard & Sheppard (1991).

Colonies are usually small, less than 50cm in diameter. Branches are short, laterally flattened and upright. Verrucae are regular and never intergrade with branches. This is the typical Pocillopora of the northern Natal reef system in South Africa: The coral is common all along the African east coast, north of Transkei.

Pocillopora eydouxi (Edwards & Haime, 1860)

Pocillopora eydouxi (Ed.& H.); Veron & Pichon (1976).

The branches in this species are more variable and longer than in the other two. Branches may be either round or flat and paddle-

shaped, the colony tends to be much bigger than in the previous two species. Verrucae are smaller than in P.verrucosa. This species has been observed in South Africa but as only small fragments were collected its presence still needs to be confirmed by further specimens.

Family **Acroporidae** Verrill, 1902

This is the biggest extant coral family encompassing the two biggest genera Acropora and Montipora. Their center of diversity is in the Indo-Pacific.

Genus **Montipora** de Blainville, 1830

This genus is common accross the Indo-Pacific. It is the second biggest hard coral genus. Although common and almost ubiquitous, Montipora are easily overlooked, as many species, especially in South East Africa, form only small or encrusting colonies. This family becomes ecologically more dominant in tropical waters. It is likely that the real number of species in this genus in South East Africa is under represented in this chapter.

Key:

1 Corallum totally or mostly glabrous (no tuberculae or papillae).....2

1* Tuberculae or papillae present.....3

2 Corallites funnel-shaped, big (around 1mm).....M.venosa (p.24)

2* Corallites flush with reticulum, small (ca. 0.6mm).....M.spongodes (p.24)

3(1*) Tuberculae and papillae small.....4

Plate 4a: Montipora venosa, 2-Mile Reef, South Africa, x2.

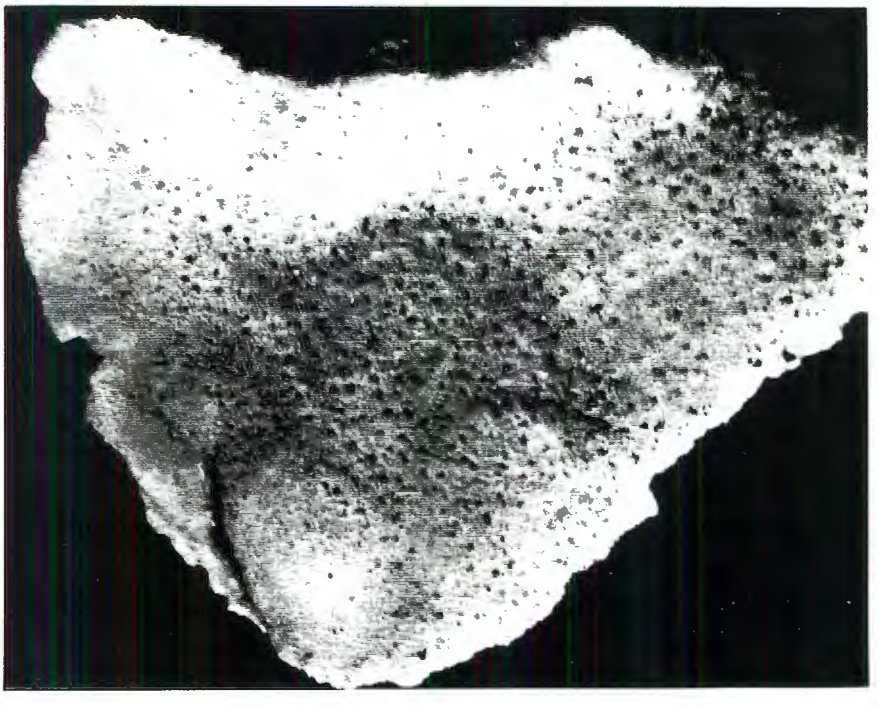


Plate 4b: Montipora spongodes, 2-Mile Reef, South Africa, x2

3* Tuberculae large, forming verrucae.....6

4(3) Papillae form a hood over corallites.....
.....M.aequituberculata (p.29)

4* Papillae do not form a hood.....5

5(4*) Papillae and tuberculae very regular, selom fuse.....
.....M.tuberculosa (p.27)

5* Papillae and tuberculae fuse regularly, often forming ridges perpendicular to growing edge.....M.monasteriata (p.29)

6(3*) Verrucae regular, do not fuse often, septa taper towards... centre of corallite .....M.verrucosa (p.27)

6* Verrucae irregular, fuse very often, septa do not taper.....M.danae (p.27)

Montipora venosa (Ehrenberg, 1834) (Plate 4a)

Montipora venosa (Ehrbg.); Veron & Wallace (1984); Sheppard & Sheppard (1991).

The corallites are immersed or exsert. The coenosteum typically, but not always, forms a funnel-shaped pit around the corallite. Corallites are relatively big (around 1mm). The reticulum is coarse and in SE-Africa papillae are rarely formed. Growth form varies from encrusting to massive. This species is recorded from South Africa (Southern Reef Complex, northern Natal) northwards.

Montipora spongodes Bernard, 1897 (Plate 4b)

Montipora spongodes Bernard; Veron & Wallace (1984)

Corallum glabrous (without papillae or tuberculae) , corallites are immersed and widely spaced. The coenosteum is completely smooth and of fine texture. This species can be differentiated

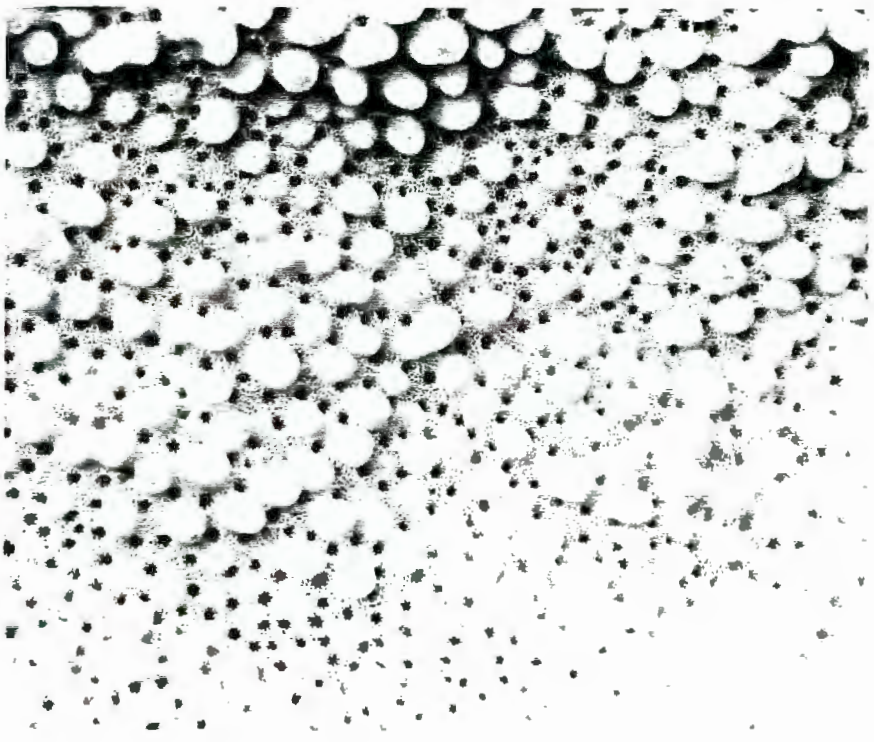


Plate 5a: Montipora verrucosa, 4-Mile Reef, South Africa, x2

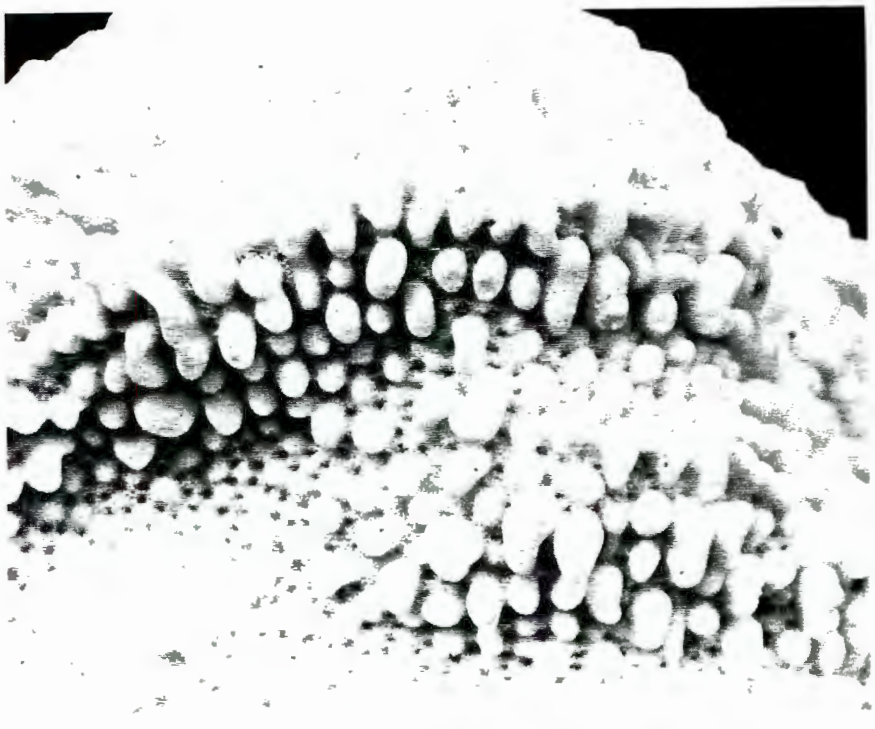


Plate 5b: Montipora danae, 4-Mile Reef, South Africa, x2

from A.venosa by its corallites which are flush with the coenosteum surface and not surrounded by a funnel-shaped pit. Growth form is encrusting to plate-like. Found from South Africa (Central Reef Complex, northern Natal) northwards.

Montipora verrucosa (Lamarck, 1816) (Plate 5a)

Montipora verrucosa (Lam.); Veron & Wallace (1984); Sheppard & Sheppard (1991).

This is one the most easily identified species of Montipora due to the very large and regular verrucae (up to 5mm diameter). Corallites are small (0.4-0.6mm diameter), immersed, always between the verrucae and with two septal cycles. The growth form is encrusting to plate-like, often forming very large colonies. It is found commonly from South Africa (Aliwal Shoal, southern Natal) northwards.

Montipora danae Edwards & Haime, 1851 (Plate 5b)

Montipora danae Ed.& H.; Veron & Wallace (1984); Sheppard & Sheppard (1991).

This species is very close to M.verrucosa and is principally distinguished by its more irregular verrucae and wider range of growth forms, from plate-like to massive. Corallites are smaller than in the previous species (up to 0.5mm) and never on the verrucae. It is uncommon in South Africa (northern Natal) and Mozambique.

Montipora tuberculosa (Lamarck, 1816) (Plate 6a)

Montipora tuberculosa (Lam.); Veron & Wallace (1984); Sheppard & Sheppard (1991).

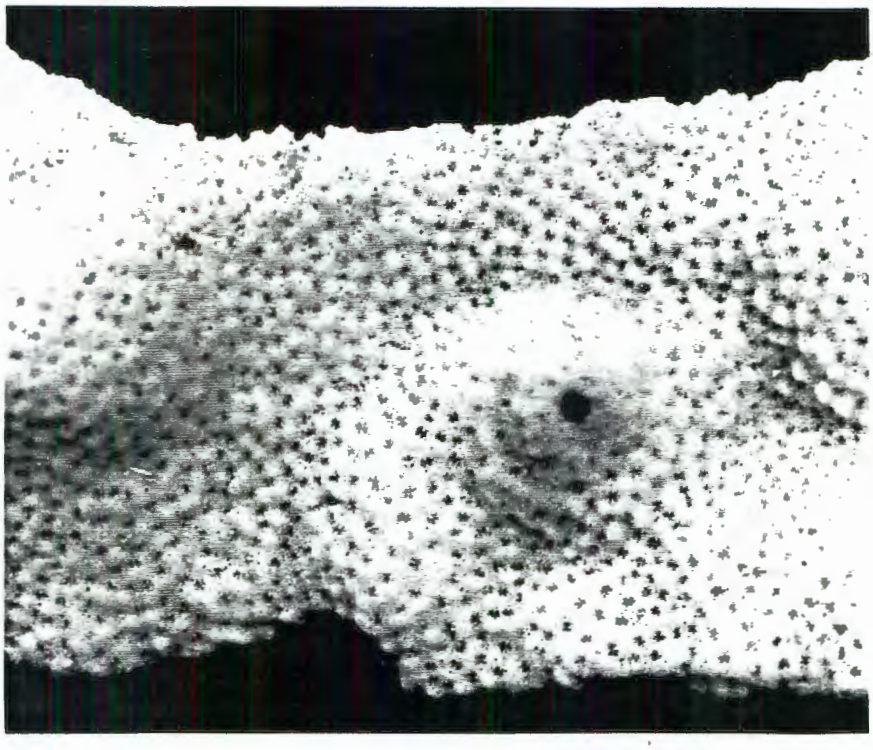


Plate 6a: Montipora tuberculosa, 2-Mile Reef, South Africa, x2

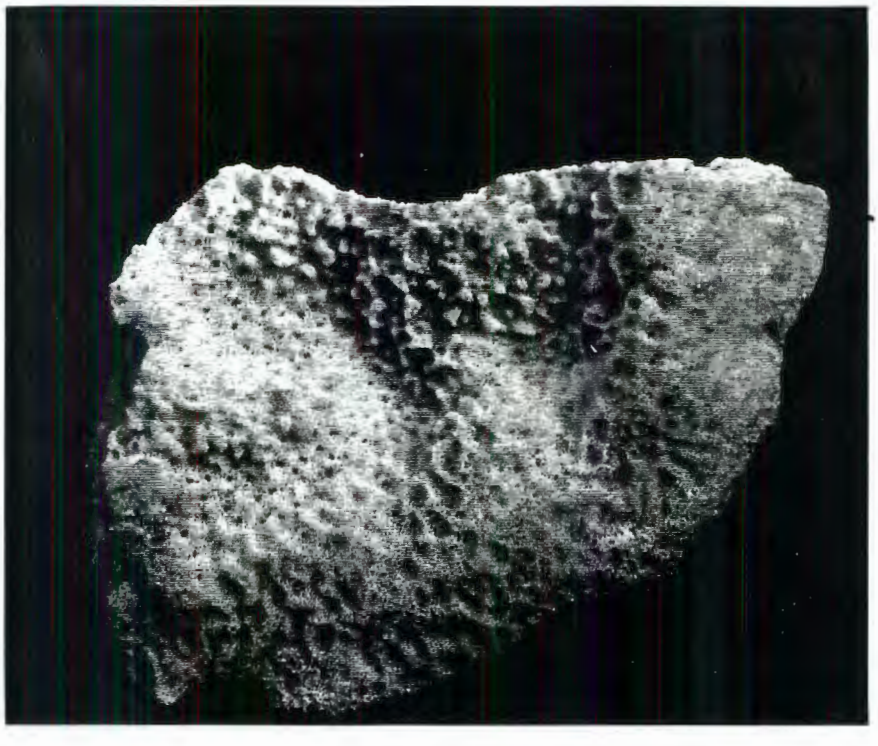


Plate 6b: Montipora monasteriata, 2-Mile Reef, South Africa, x2

Corallites immersed to exsert and surrounded by papillae. Tuberculae of about 1 corallite diameter as well as papillae present but these do not fuse as regularly as in the following species. Corallite diameter is around 0.7mm. Growth form encrusting, submassive to plate-like. This is one of the most common Montipora species, found from South Africa (Aliwal Shoal, southern Natal) northwards.

Montipora monasteriata (Forskal, 1775) (Plate 6b)

Montipora monasteriata (Forsk.); Veron & Wallace (1984); Sheppard & Sheppard (1991).

This species is close to M.tuberculosa, but its tuberculae and papillae often fuse perpendicular to the growing edge. Calices are around 0.6mm. Growth form is plate-like to massive, plates can be bifacial. It is found from South Africa (northern Natal) northwards.

Montipora aequituberculata Bernard, 1897 (Plate 7a)

Montipora aequituberculata Bernard; Veron & Wallace (1984).

Corallites exsert to immersed, surrounded by thecal papillae, which can form hoods. This distinguishes this species from all other local Montipora. Growth form is foliose. From South Africa (northern Natal) northwards.

Genus **Acropora** Oken, 1815

This is the biggest scleractinian coral genus and is found word-wide. In South-East Africa some 30 species are encountered, which are dealt with in great detail in their own monograph, where an identification key is provided (Part I Chapters 2 & 4).

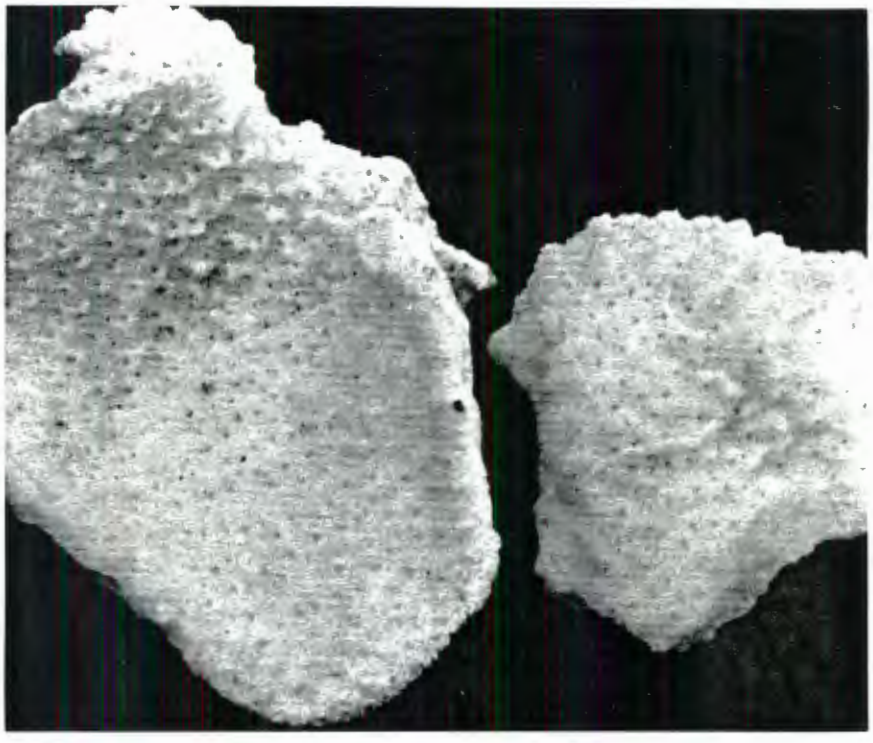


Plate 7a: Montipora aequituberculata, 2-Mile Reef, South Africa, x2

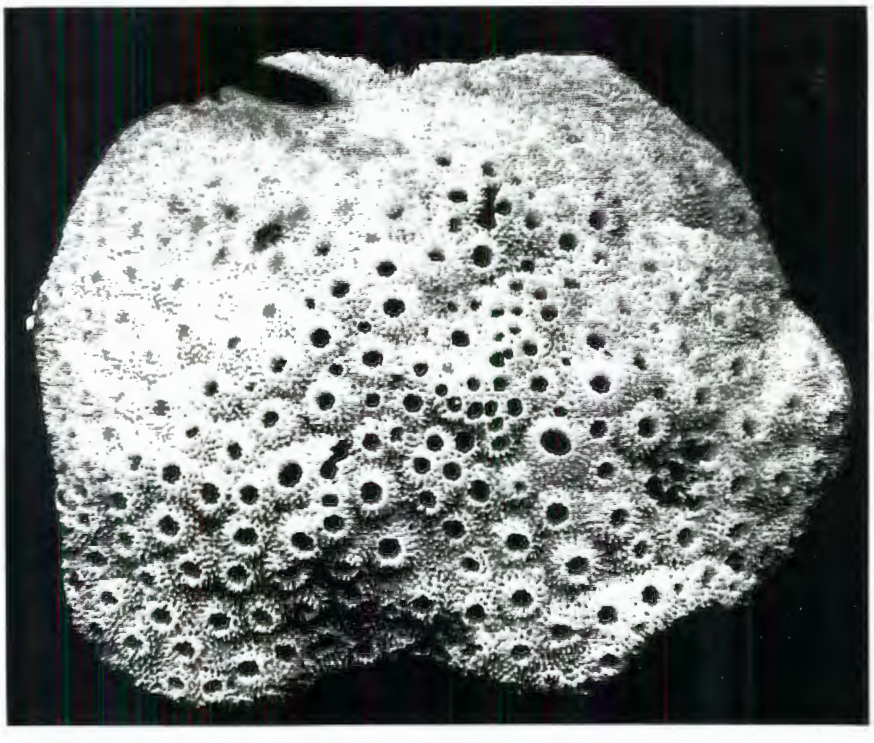


Plate 7b: Astraeopora myriophthalma, 2-Mile Reef, South Africa, x0.75

The following species were recorded in South Africa:

Acropora palifera, A. humilis, A. clathrata, A. nasuta, A. tenuis, A. millepora, A. austera, A. aculeus, A. latistella, A. danai, A. florida, A. horrida, A. anthocercis, A. hyacinthus and four hitherto undescribed species (see Part I, Chapter 3).

The following species were recorded only in Mozambique:

A. gemmifera, A. monticulosa, A. formosa, A. microphthalma, A. cf. striata, A. cytherea, A. nana, A. valida, A. secale.

Genus **Astraeopora** Blainville, 1830

Only one species of this very conspicuous genus has so far been found in our area.

Astraeopora myriophthalma (Lamarck, 1816) (Plate 7b)

Astraeopora myriophthalma (Lam.); Scheer & Pillai (1983); Veron & Wallace (1984); Sheppard & Sheppard (1991).

Colonies are massive and mostly hemispherical. Corallites are exsert and deep and either lack, or have very rudimentary septa. The coenosteum is densely covered by coarse, elaborate spicules. Recorded from northern Natal northwards.

Family **Poritidae** Gray, 1842

This world-wide distributed family is a very important member of almost every single reef system in the world and some of its species are among the dominant frame-builders on Indo-Pacific reefs. It is treated in graeter detail in Part I, Chapter 6. The South African species are:

Porites lichen, P. solida, P. lutea; P. nigrescens; Goniopora djiboutensis, G. crassa, G. somaliensis; Alveopora allingi, A. spongiosa.

Species found exclusively in Mozambique are:

Porites cylindrica, P. lobata, P. compressa; Goniopora stokesi, G. lobata.

Family **Siderastreidae** Vaughan & Wells, 1943

This family seems to have its center of diversity in the Arabian region (Sheppard & Sheppard, 1991). It could therefore also be expected to be well represented in East Africa. Four of its seven genera have been found in South East Africa.

Genus **Psammocora** Dana, 1846

This genus was previously included with the Thamnasteriidae, but since Veron (1986) it is generally accepted as a Siderastraeid (Veron & Marsh, 1988; Veron, 1990; Sheppard & Sheppard, 1991).

Psammocora haimeana Edwards & Haime, 1851 (Plate 8a)

Psammocora haimeana Edwards & Haime, 1851; Veron & Pichon (1976).

Psammocora nierstraszi Horst, 1921; Scheer & Pillai (1983).

Psammocora profundacella Gardiner, 1898; Scheer & Pillai (1983); Veron (1986).

Psammocora superficialis Gardiner, 1898; Veron (1986).

Sheppard & Sheppard (1991) put all the above mentioned species into synonymy with P. haimeana. I agree with this step, as Southern African material also does not allow distinctions to be

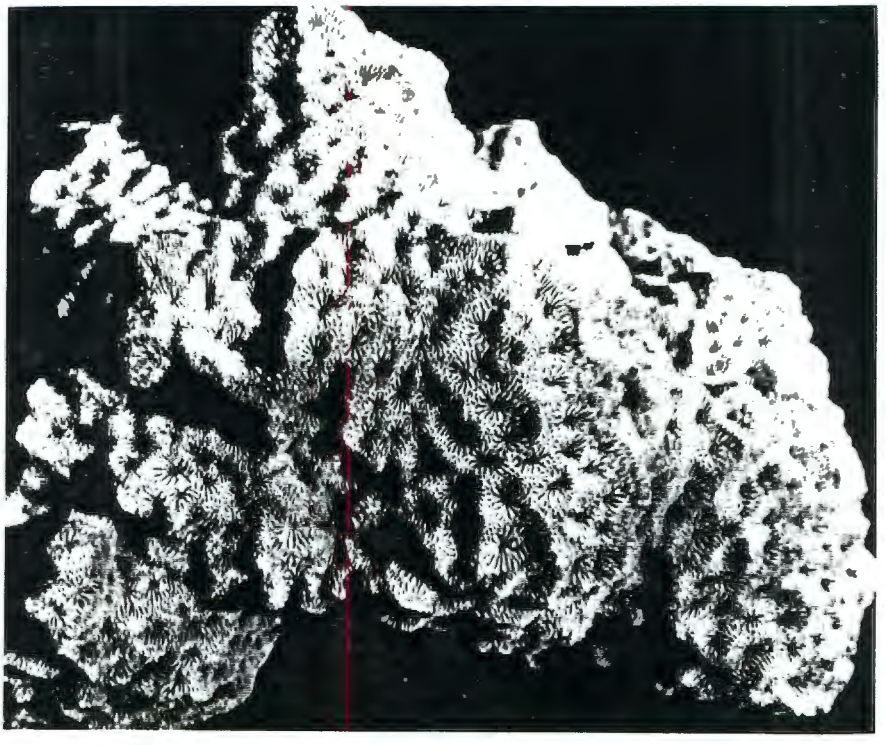


Plate 8a: Psammocora haimeana, Chaka's Rock, South Africa, x1.5

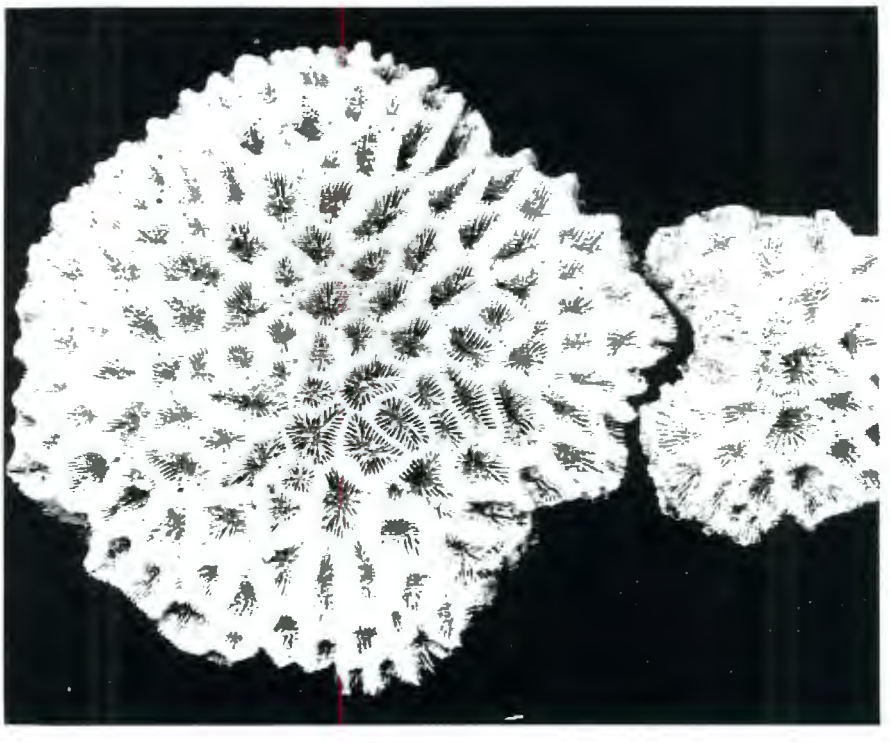


Plate 8b: Anomastrea irregularis, Jesser Point, South Africa, x2

drawn between these species. Colonies vary from encrusting to massive and are common from the intertidal to greater depths. Found from southern Natal, possibly also Transkei, northwards.

Genus **Anomastrea** von Marenzeller, 1901

The single species in this genus was previously believed to occur only in Eastern Africa, but Sheppard & Sheppard (1991) recorded it as far north as the Persian Gulf.

Anomastrea irregularis von Marenzeller, 1901 (Plate 8b)

Anomastrea irregularis Marenz.; Veron (1986); Sheppard & Sheppard (1991)

Growth form is encrusting to massive. Corallites are cerioid and small (around 3mm) with numerous (about 30) septa with fine dentations. Septa often fuse before they reach the columella, which is small. In the intertidal, where it is very common, most colonies are rather flat. This species is most common in tidal pools and not frequently seen on the subtidal reefs. Calices are small, with a deep fossa and numerous septa, which often fuse. Found from Transkei northwards.

Genus **Coscinaraea** Edwards & Haime, 1848

This genus is widespread in the Indo-Pacific and common in South East Africa. The two species in our region are easily seperated by corallite size.

Coscinaraea monile (Forskal, 1775) (Plate 9a)

Coscinaraea monile (Forsk.); Scheer & Pillai (1983); Sheppard & Sheppard (1991).

Plate 9a: Coscinaraea monile, 2-Mile Reef, South Africa, x1

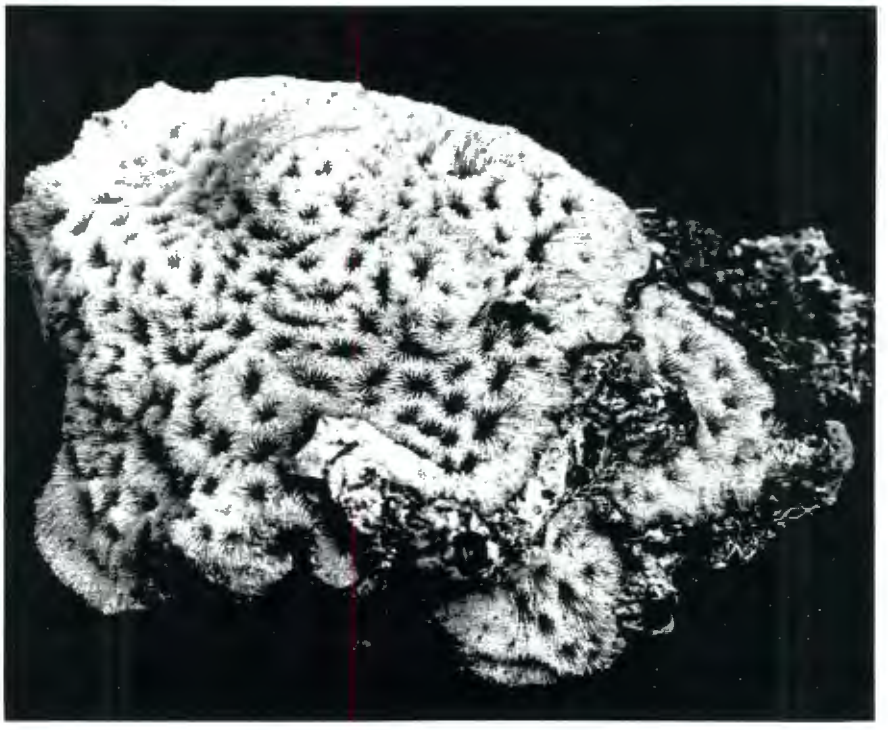


Plate 9b: Coscinaraea columna, 4-Mile Reef, South Africa, x1

This species is common, particularly on the deeper parts of the reefs. Its corallites are shallow with wide walls and continuous costae between them. Corallites often fuse to form short series, but the normal condition is monocentric. Growth form is massive, usually in low humps. Occurs from northern Natal (Southern Reef Complex) northwards.

Coscinaraea columna (Dana, 1846) (Plate 9b)

Coscinaraea columna (Dana): Veron & Pichon (1980); Sheppard & Sheppard (1991).

The smaller corallites and deeper fossae separate this species well from C.monile. In C. cloumna most corallites fuse to form short series, parallel to the growing edge. The corallite walls are narrower and higher than in C.monile and the septa plunge steeply into the calyx. This species is more common in South Africa than C.monile. Growth form is massive, sometimes with almost laminar edges. Columnar growth form (Veron, 1986) was never observed in South African specimens. It is found from central Natal northwards.

Genus **Horastrea** Pichon, 1971

This genus has been discovered in Madagascar and it seems to be confined to the western Indian Ocean.

Horastrea indica Pichon, 1971. (Plate 10a)

Growth form massive, usually small colonies, diameter up to 10cm. Corallites are plocoid to submeandroid on Mozambiquan specimens but subcerioid on South African specimens. These situations can intergrade on the same specimen. Corallites are wide and shallow,

Plate 10a: Horastrea indica, Inhaca Island, Mozambique, x1

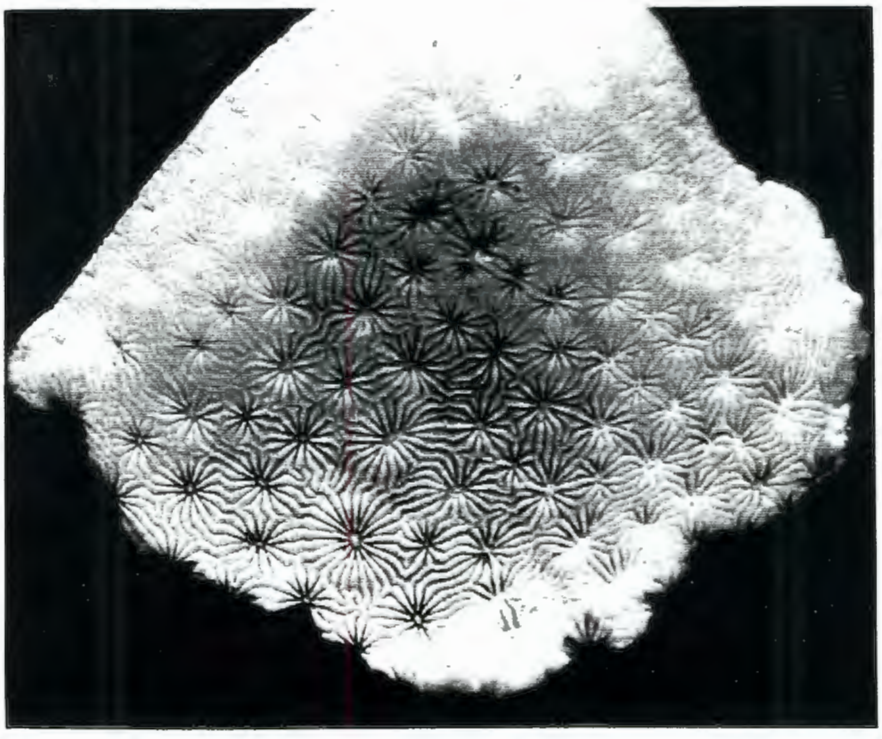


Plate 10b: Pavona clavus, 2-Mile Reef, South Africa, x4

with septa in three orders and well developed septocostae. This is a common coral in South Africa, especially on sandy areas of the reefs. Found from northern Natal (Southern Reef Complex) northwards.

Family **Agariciidae** Gray, 1846

The members of this family can be easily identified by the mostly poorly defined thecae and continuous costae, which run continuously between adjacent corallites and can form very attractive patterns. Growth form varies from massive to foliaceous. Although present on most reefs, they are hardly ever common.

Genus **Pavona** Lamarck, 1801

This genus is very obvious due to their plocoid corallites which are connected by well developed, continuous costae, which often create a strikingly beautiful pattern.

Pavona clavus (Dana, 1846) (Plate 10b)

Pavona clavus (Dana); Veron & Pichon (1980); Veron (1986).

This species can easily be identified by its small, shallow corallites (2-3mm), which give the corallum a very smooth appearance. Septa tend to radiate from the centre of each corallite. There are no ridges developed as in the other two species. Growth form massive, columnar or laminar. From northern Natal northwards. This identification requires further verification.

Pavona minuta Wells, 1954 (Plate 11a)

Pavona minuta Wells; Veron & Pichon (1980); Veron (1986);

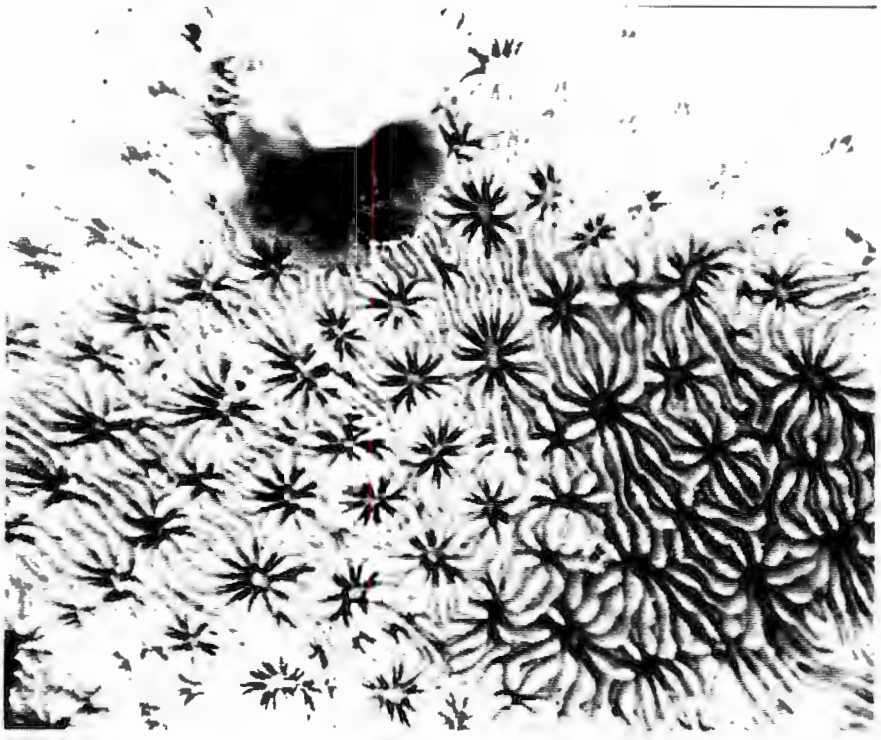


Plate 11a: Pavona minuta, 2-Mile Reef, South Africa, x5

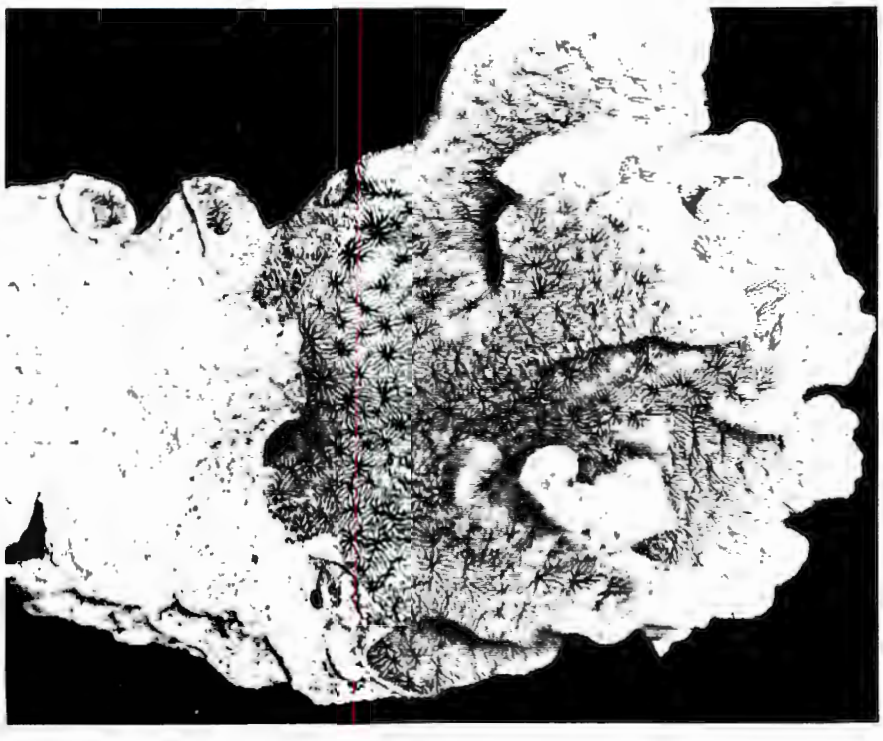


Plate 11b: Pavona decussata, Inhaca Island, Mozambique, x0.75

Sheppard & Sheppard (1991).

This species has even smaller corallites than P.clavus (around 2mm). It has more exsert septocostae than the previous species and they tend to run more parallel. The colonies often form wide ridges. Rare. From northern Natal northwards. This identification requires further verificatio

Pavona decussata (Dana, 1846) (Plate 11b)

Pavona decussata (Dana); Veron & Pichon (1980); Veron (1986); Sheppard & Sheppard (1991).

The numerous acute ridges formed by this species on the surface make it easily identifiable. Extremes in growth form vary from almost flat to almost totally composed of bifacial fronds. Corallites are well spaced with continuous costae. Corallite diameter around 3mm. Not recorded in South Africa. Mozambique only, but common in sheltered areas on Inhaca Island.

Pavona maldivensis (Gardiner, 1905) is a further species occurring commonly in Mozambique from Inhaca Island northwards, but not in South Africa. It is easily identified by its large, plocoid corallites and columnar colonies often growing to several metres in diameter. It is not illustrated as no museum material was available.

Genus **Leptoseris** Edwards & Haime, 1849

The corals of this genus are characteristically foliaceous and typically found in the deeper areas of the reefs.

Leptoseris explanata Yabe & Sugiyama, 1941 (Plate 12a)

Leptoseris explanata Yabe & Sugiyama; Veron & Pichon (1980); Veron (1986); Sheppard & Sheppard (1991).

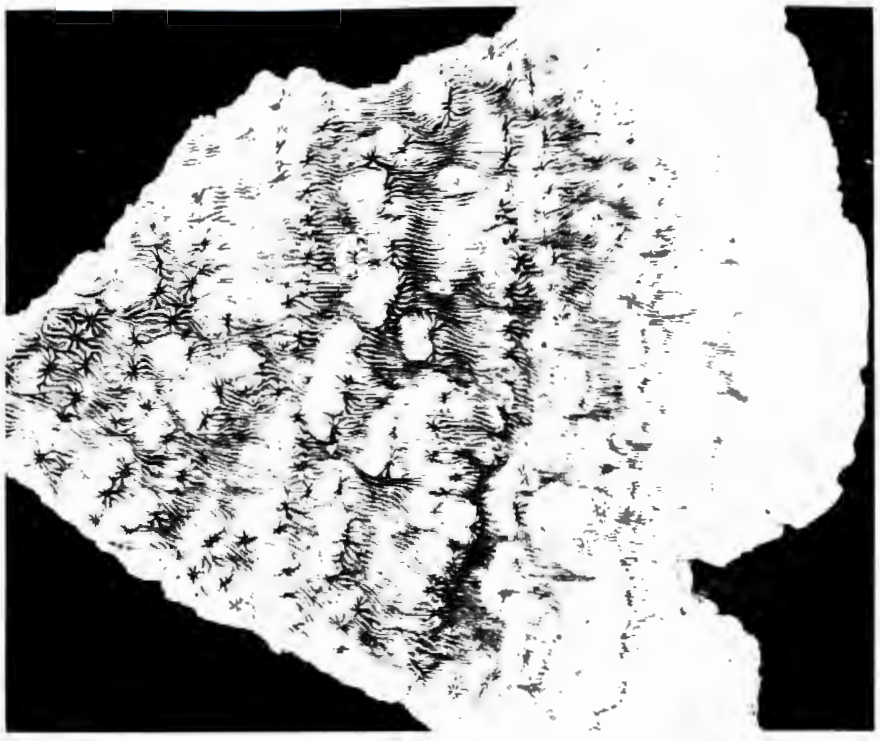


Plate 12a: Leptoseris explanata, 4-Mile Reef, South Africa, x0.5

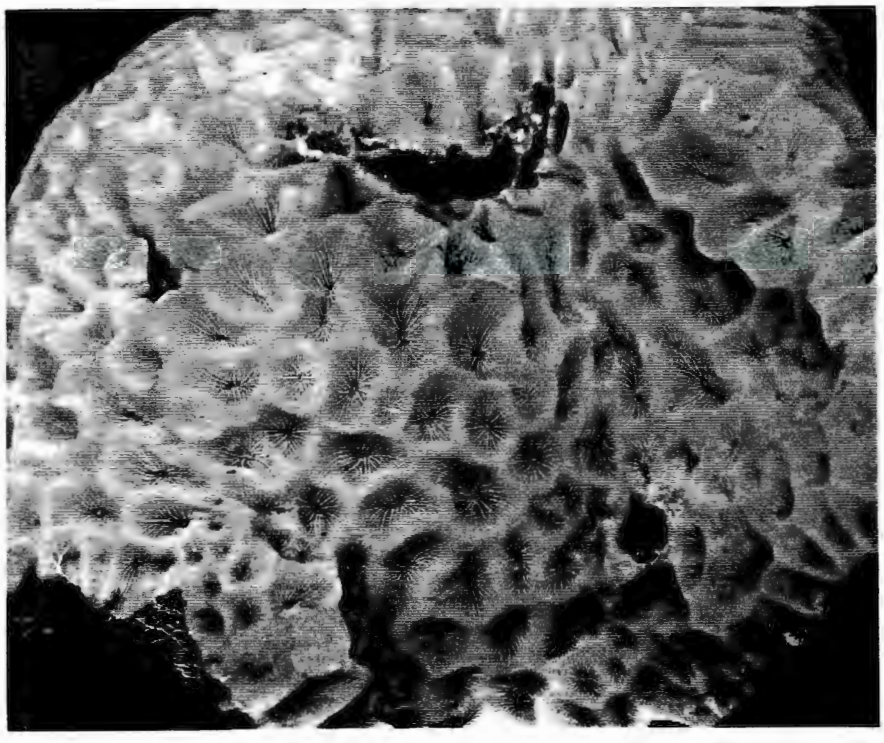


Plate 12b: Gardineroseris planulata, 2-Mile Reef, South Africa, x1.5

This coral is easily identified by its foliaceous growth form and the large, widely spaced, outwardly inclined corallites, which are connected by continuous septocostae, most of which run parallel to each other and perpendicular to the growing edge. The septocostae are arranged in alternating size classes. The species is not rare, but generally confined to depths below 20m or shady places at lesser depths. It is found from northern Natal northwards.

Genus **Gardineroseris** Scheer & pillai, 1974

There is only one species in this genus, which is widespread in the Indo-Pacific.

Gardineroseris planulata (Dana, 1846) (Plate 12b)

Gardineroseris planulata (Dana); Veron & Pichon (1980); Scheer & Pillai (1983); Veron (1986); Sheppard & Sheppard (1991).

This species is characterised by small,(3-5mm) very irregular and deep calices with about 50 septa, which show various degrees of fusion. The growth form is massive and colonies may grow to considerable size, sometimes a metre or more in diameter, although most colonies are small. This species is not common, but present on most reefs from northern Natal (Southern Reef Complex) northwards.

Genus **Coeloseris** Vaughan, 1918

There is only one species in this genus, which has previously only been recorded from the Eastern Indian Ocean and the Pacific (Veron, 1986).

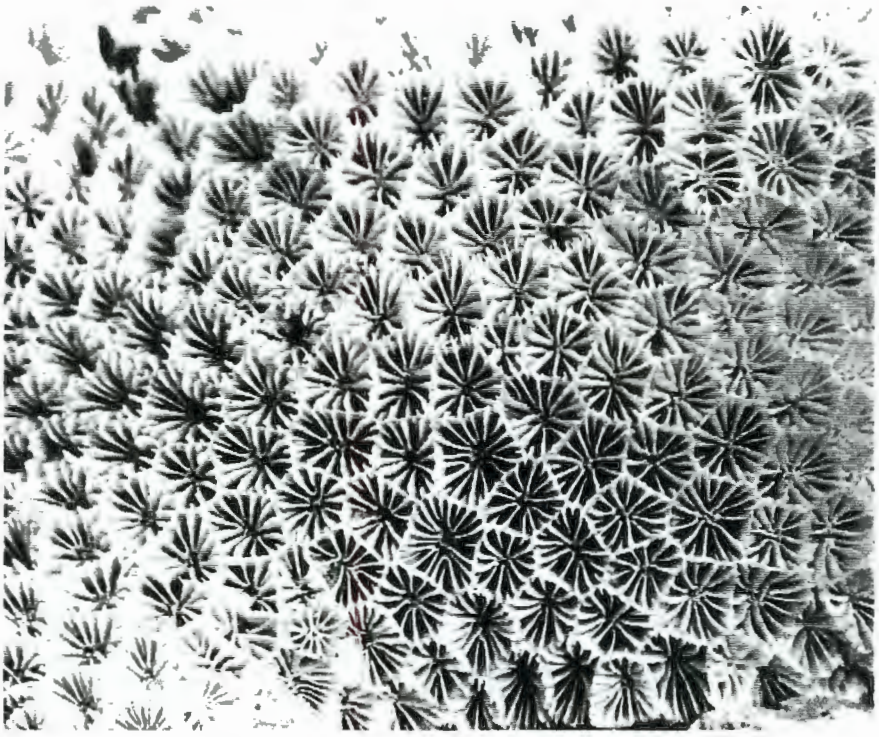


Plate 13a: Coeloseris mayeri, Inhaca Island, Mozambique, x2

Plate 13b: Pachyseris speciosa, 4-Mile Reef, South Africa, x0.7

Coeloseris mayeri Vaughan, 1918 (Plate 13a)

Coeloseris mayeri Vaughan; Veron & Wallace (1980); Veron (1986).

This species is very conspicuous due to its deep, polygonal calyces with thin and acute thecae, smooth septa and missing columellae. On first sight it resembles the faviid Goniastrea, but can be told apart by the different structure of the septa, these being only finely granulated or smooth in Coeloseris and missing the paliform lobe, which is typical for Goniastrea. The colonies are massive and can attain a large size. It is rare and occurs from northern Natal (Southern Reef Complex) northwards.
This identification requires further verification.

Genus Pachyseris Edwards & Haime, 1849

The typical feature of this genus are the long meandroid valleys without seperated centres, which gives the corals their common name "disc-coral". It is debatable whether there are two or only one species in the genus (Veron & Pichon, 1980; Sheppard & Sheppard, 1991).

Pachyseris speciosa (Dana, 1846) (Plate 13b)

Pachyseris speciosa (Dana); Veron & Pichon (1980); Veron (1986); Sheppard & Sheppard (1991).

?Pachyseris rugosa (Lamarck, 1801); Veron & Pichon (1980); Scheer & Pillai (1983):

Sheppard & Sheppard (1991) merged the two species in this genus P.speciosa and P.rugosa. Material from South East Africa does not allow comment on the validity of the argument, as the species are rare and not enough material is available. Pachyseris is easily

recognized by the long valleys, which may be contorted or very straight. It is very rare in South Africa and confined to the deep parts of reefs. Sofar it has been recorded from northern Natal (Central Reef Complex) northwards.

Family **Fungiidae** Dana, 1846

All exept one member of this family are free living, unattached discs. They are common in some parts of the reefs. In South Africa they can be found in greatest abundance on the deep parts of the reefs. From Inhaca Island northwards there is a great increase in their diversity.

Key:

1 Corallum free-living.....2

1* Corallum attached & funnel shaped.....Podabacia (p.53)

2(1) Corallum solitary or with only a few interconnected polyps lying in a central groove; septa very long and radiating.....3

2* Corallum colonial, numerous polyps scattered over the surface, septa short and petaloid.....Polyphyllia (p.50)

3(2) Disc distorted into sections due to incipient asexual budding.....Diaseris (p.48)

3* Disc in one entity.....4

4(3) Disc roundly oval, with one central gastral cavity.....5

4* Disc elongated with a few gastral cavities in the central groove and also between lateral septa.....Herpolitha (p.50)

5(4) Corallum small (20-40mm) with fine septal teeth and costal spines.....Cycloseris (p.45)

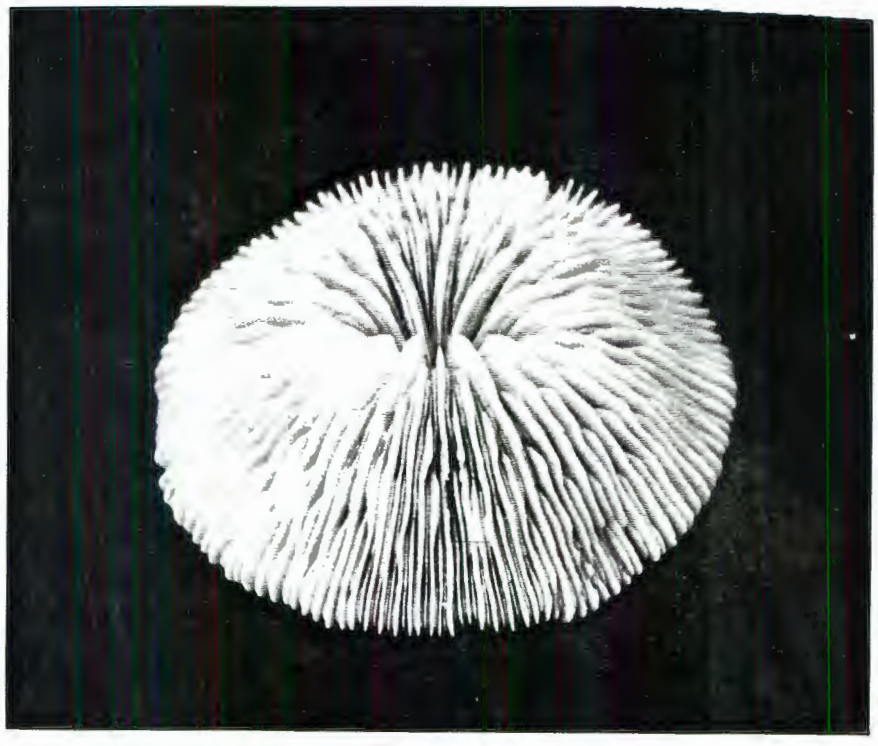


Plate 14a: Cycloseris cyclolites, 4-Mile Reef, South Africa, x1.5

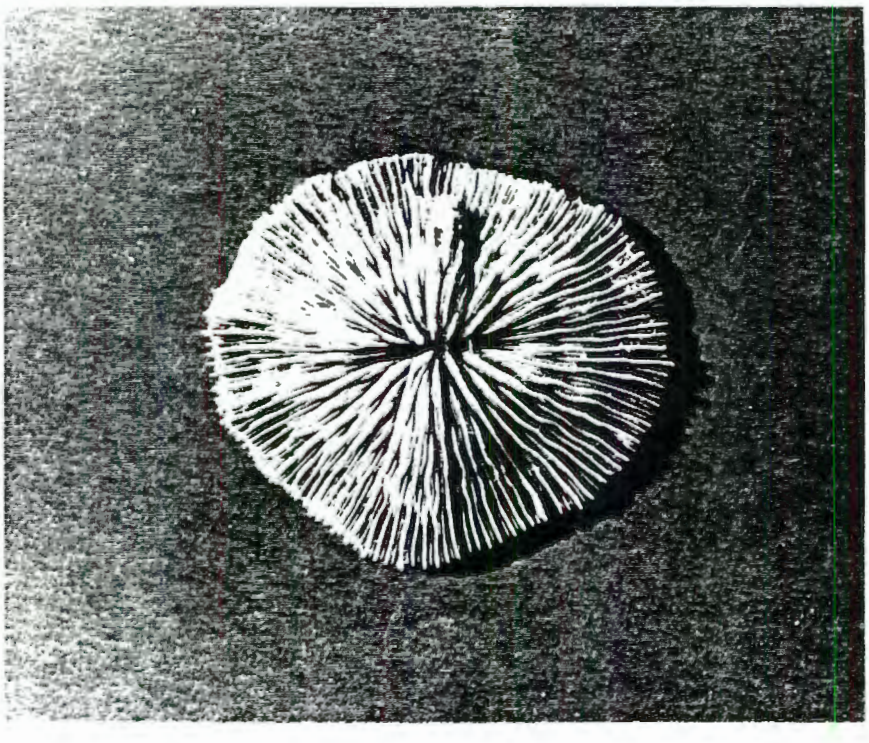


Plate 14b: Cycloseris costulata, 7-Mile Reef, South Africa, x1

5* Corallum large, with coarse septal teeth and costal spines.....
.....Fungia (p.48)

Genus **Cycloseris** Edwards & Haime, 1849

Solitary, mostly neatly round or slightly oval. They can be easily told apart from the other fungiids by their smooth septa, unperforated discs and generally smaller size.

Cycloseris cyclolites (Lamarck, 1801) (Plate 14a)

Cycloseris cyclolites (Lam.; Veron & Pichon (1980); Scheer & Pillai (1983); Veron (1986); Sheppard & Sheppard (1991).

This is the most common species in South Africa, with a circular disc, concave to flat undersurface and a strongly convex upper surface. The mouth fossa is elongate. Costae are well developed on the peripheral part, but thin in the centre. Common in northern Natal and Mozambique.

Cycloseris costulata (Ortmann, 1899) (Plate 14b)

Cycloseris costulata (Ortm.); Veron & Pichon (1980); Scheer & Pillai (1983); Veron (1986); Sheppard & Sheppard (1991).

The undersurface is mostly flat to slightly concave, the upper part is only arched around the fossa, but flat on the edges, unlike the previous species, where the whole upper part is convex. The mouth fossa is elongate. Common in northern Natal, South Africa.

Cycloseris marginata (Boschma, 1923) (Plate 15a)

Cycloseris marginata (Boschma); Scheer & Pillai (1974); Veron & Pichon (1980); Veron (1986); Sheppard & Sheppard (1991).

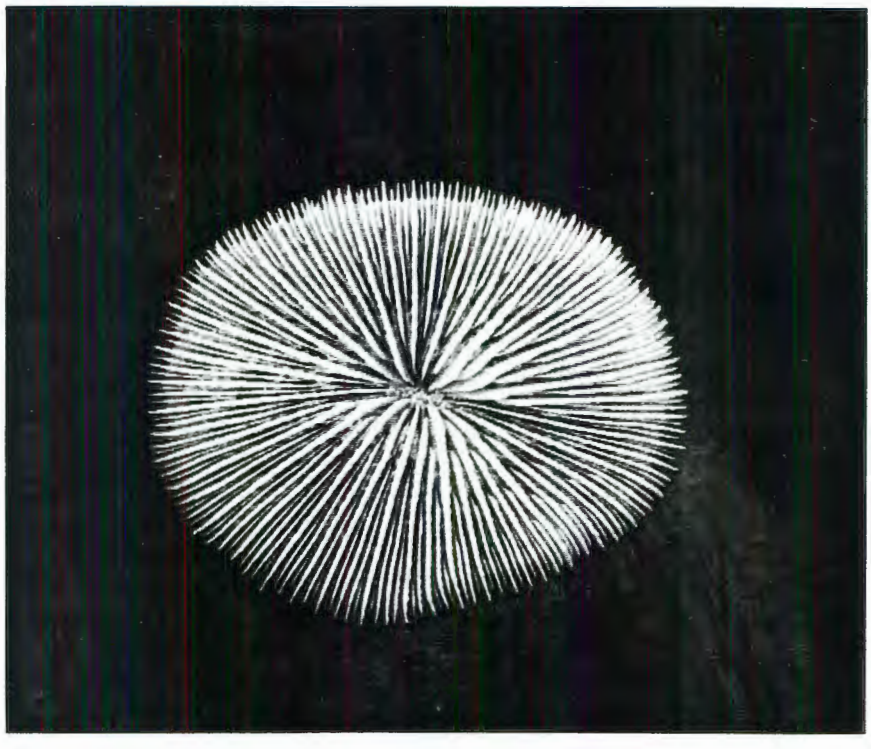


Plate 15a: Cycloseris marginata, 7-Mile Reef, South Africa, x1

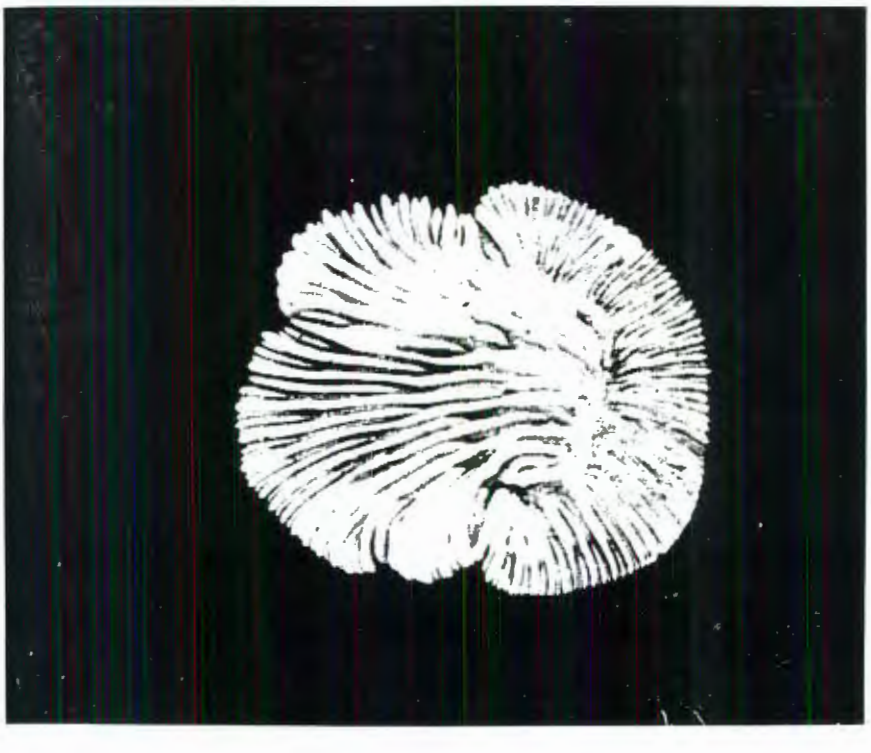


Plate 15b: Diaseris distorta, 2-Mile Reef, South Africa, x1.5

The shape is more irregular and corallites tend to be smaller and less calcified than in the previous two species. The undersurface is convex with a clear attachment scar in the centre. The upper surface is flat to slightly concave. Uncommon, from northern Natal northwards.

Genus **Diaseris** Edwards & Haime, 1849

Of this small genus, which is related to Cycloseris (Veron, 1986), only one species is found in South Africa. The species in this genus reproduce asexually by autotomy (Veron, 1986), which also provides a good identification clue, as most coralla are either incomplete or busy forming wedge shaped daughter colonies, ready to break off.

Diaseris distorta (Michelin, 1843) (Plate 15b)

Diaseris distorta (Michelin); Veron & Pichon (1980); Veron (1986).

The specimens found in South Africa were small, with a diameter around 3cm. They consist of three fan-shaped segments of unequal size. The mouth fossa is elongate and at the junction of the segments. Septa are unequal. This species is apparently rare in South Africa and was only found on the deep parts of the reefs in northern Natal (Central Reef Complex).

Genus **Fungia** Lamarck, 1801

All Fungia species consist of free-living discs. They are generally larger in size than the previously discussed genera. The

Plate 16a: Fungia (Pleuractis) scutaria, 4-Mile Reef, South Africa, x0.5

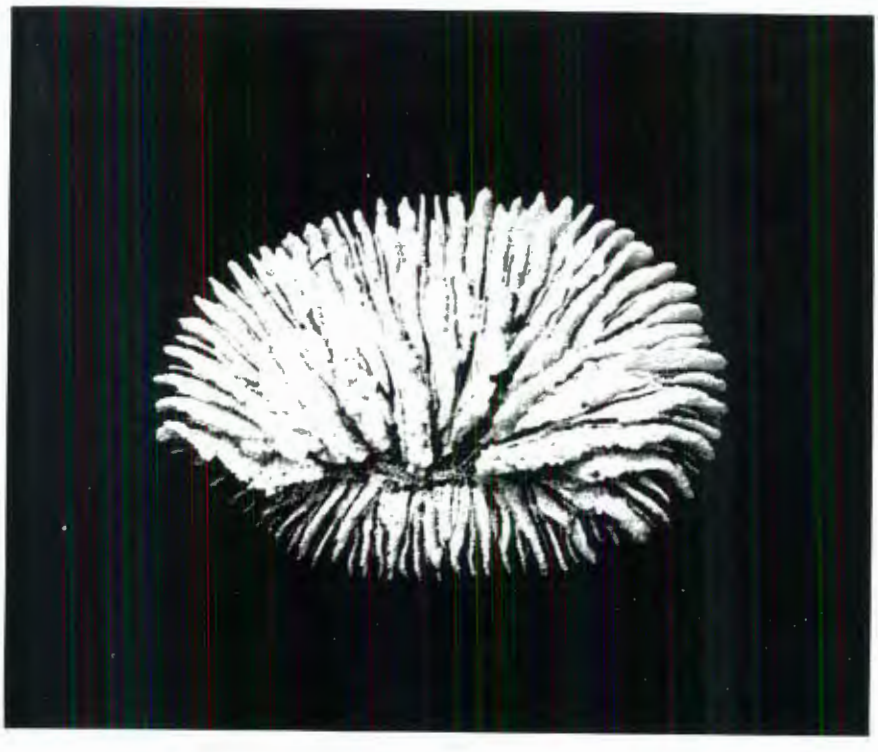


Plate 16b: Fungia (Danafungia) scruposa, Inhaca Island, Mozambique, x1

genus is large and diverse, divided into five distinct subgenera. Only one is found in South Africa.

Subgenus **Pleuractis** Verrill, 1864

One species of this genus is found in South Africa. It is the most common and conspicuous of all local Fungiidae.

Fungia (Pleuractis) scutaria Lamarck, 1801. (Plate 16a)

Fungia (Pleuractis) scutaria Lam.; Veron & Pichon (1980); Scheer & Pillai (1983); Sheppard & Sheppard (1991).

Corals are elongate, thick and heavy. The primary septa bear characteristic lobes, where tentacles originate in the live animal. Septa are finely serrated. Diameter up to 20cm. Very common on all reefs in northern Natal.

The subgenus **Danafungia** is only found in Mozambique with one species (**Fungia (Danafungia) scruposa** Klunzinger, 1879, Plate 16b). It is easily recognized by its spiny and irregular appearance. Also the subgenus **Verillofungia** is only found from Inhaca Island nortwards (Plate 17a), with one species (**Fungia (Verillofungia) concinna** Verrill, 1864) sofar recorded. It is very regular in appearance, with clearly alternating septa and costae. The septal and costal spines of **Verillofungia** are smaller and more regular than in **Danafungia** (Veron, 1986). Other free-living fungiid genera found only in Mozambique are **Herpolitha** (Plate 17b) and **Polyphyllia** (Plate 18a), Both are colonia. **Polyphyllia** is easily recognized by its numerous evenly distributed, small corallites with petaloid septa. **Herpolitha** are elongate colonies

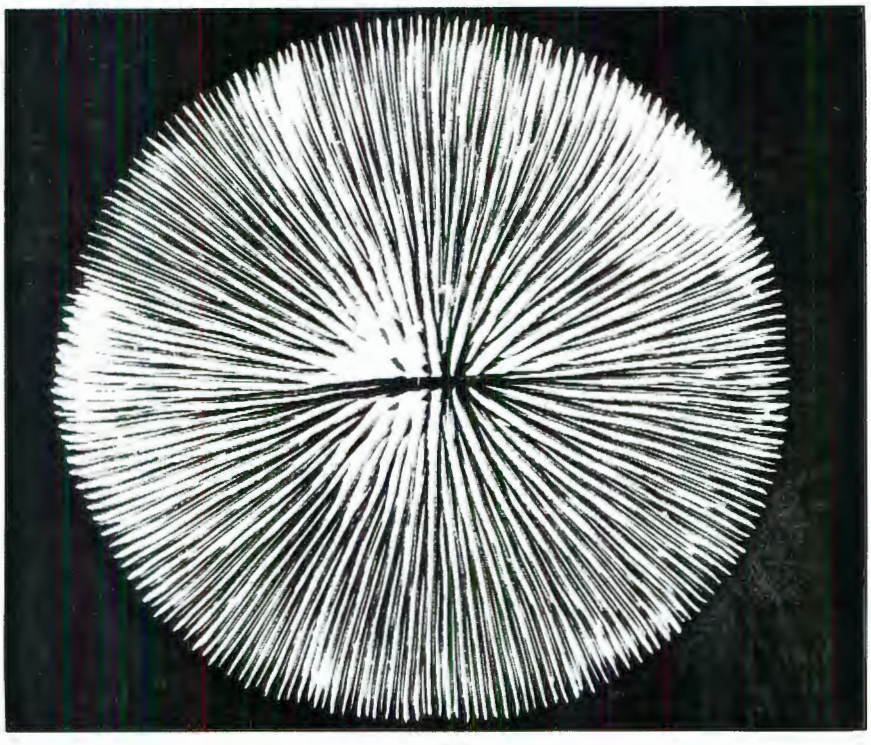


Plate 17a: Fungia (Verillofungia) concinna, Inhaca Island, Mozambique,x0.

Plate 17b: Herpolitha limax, Inhaca Island, Mozambique, x0.5

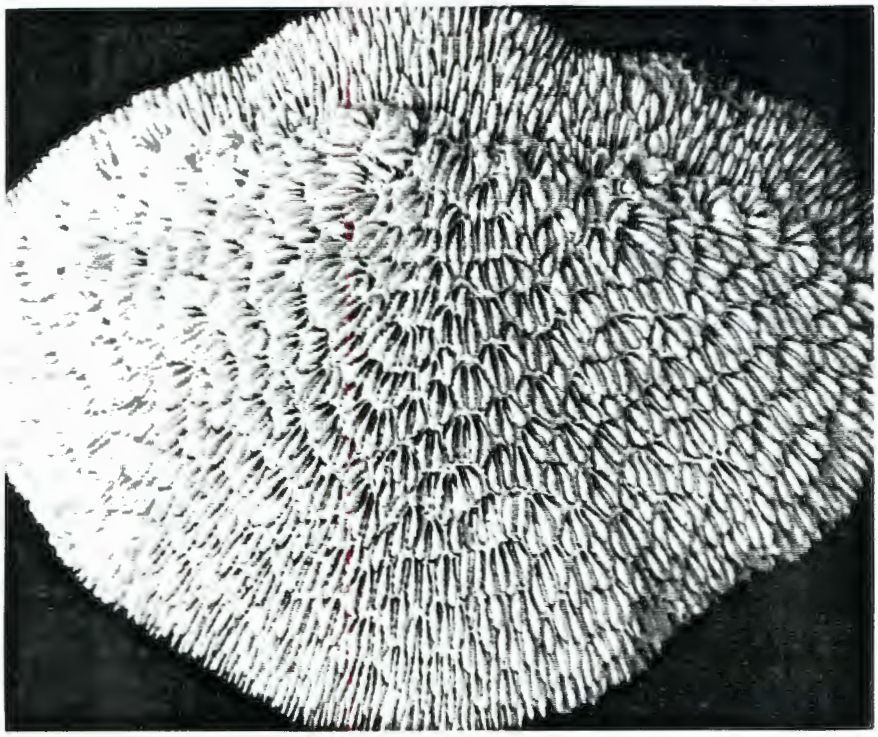


Plate 18a: Polyphyllia talpina, Inhaca Island, Mozambique, x0.75

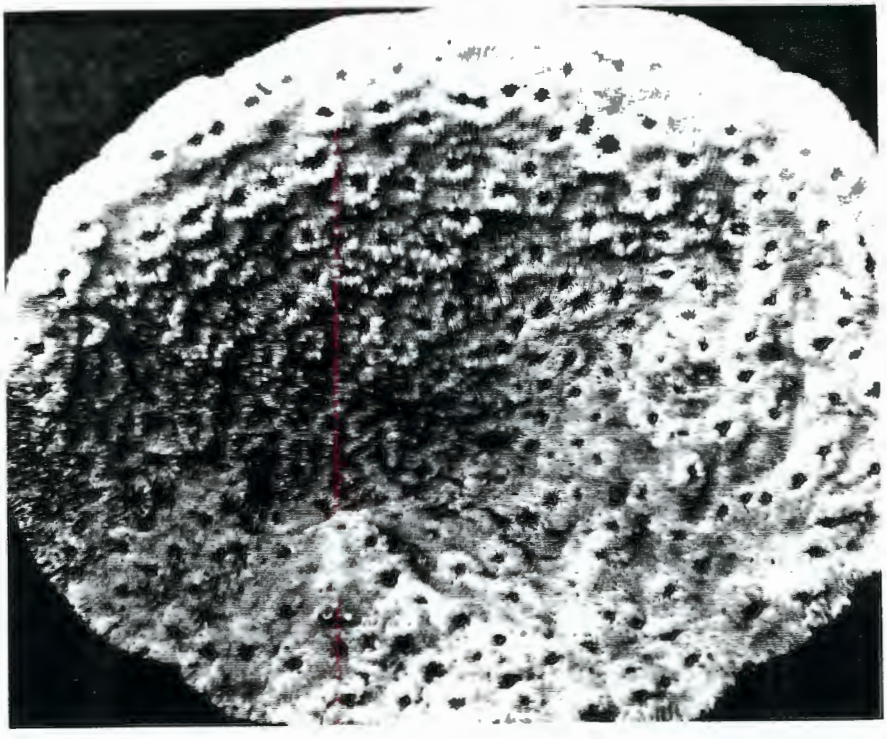


Plate 18b: Podabacia crustacea, Red Sands Reef, South Africa, x0.75

with a central groove and sometimes lateral grooves. Coralla are often long and distorted.

Genus Podabacia Edwards & Haime, 1849

This is the only attached genus within the Fungiidae found in South Africa.

Podabacia crustacea (Pallas, 1766) (Plate 18b)

Podabacia crustacea (Pallas); Veron & Pichon (1980); Scheer & Pillai (1983); Sheppard & Sheppard (1991).

Foliaceous, unifacial, in South Africa mostly forming vasiform colonies. Calices are around 4mm diameter and well seperated, often (especially in smaller colonies) a central corallite can be distinguished. Septa and costae alternate in height and thickness and are dentate. This species is uncommon and only found on deep or shaded parts of the reefs. From northern Natal (Southern Reef Complex) northwards.

Family Oculinidae Gray, 1847

There is only one zooxanthellate genus in this family (Sheppard & Sheppard, 1991), which is common in South Africa.

Genus Galaxea Oken, 1815

This genus is typical of high latitude reefs and turbid environments, where it is common all over the Indo-Pacific (Veron, 1986).

Galaxea fascicularis (Linnaeus, 1767) (Plate 19a)

Galaxea fascicularis (L.); Veron & Pichon (1980); Scheer &

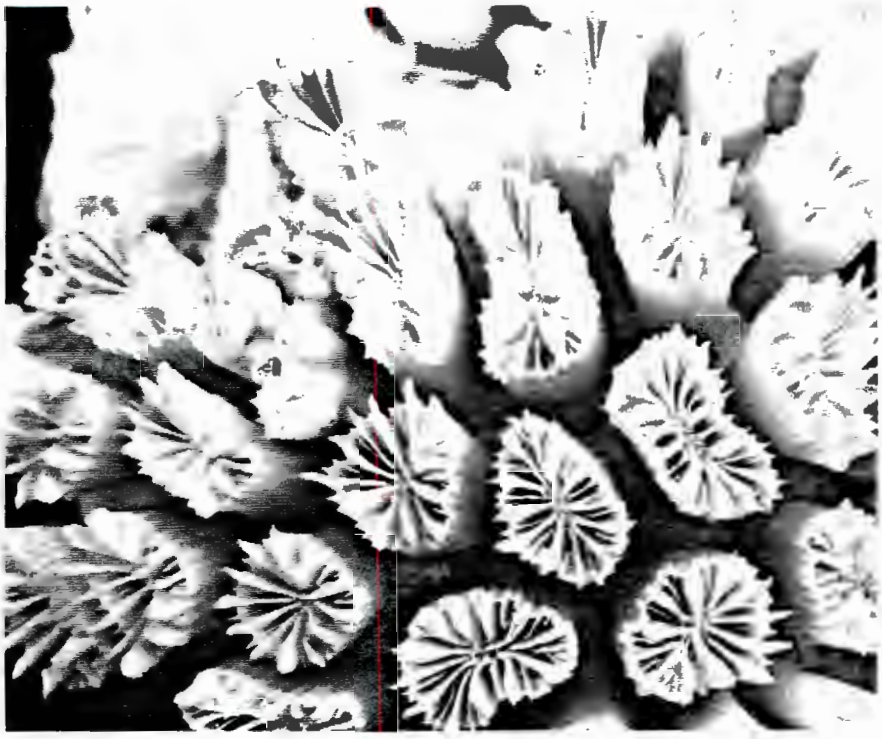


Plate 19a: Galaxea fascicularis, 2-Mile Reef, South Africa, x1.5

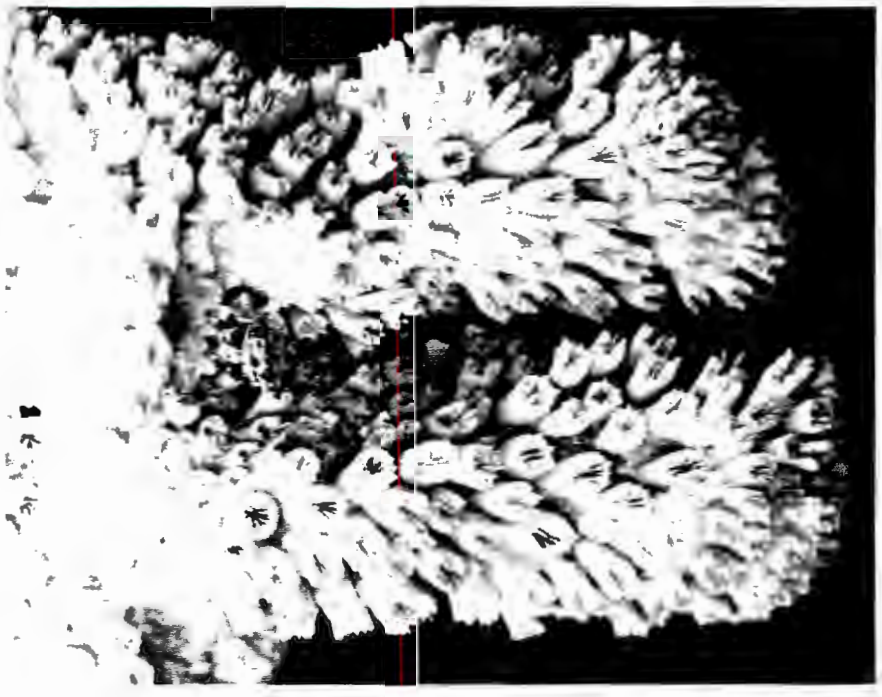


Plate 19b: Galaxea astreata, Inhaca Island, Mozambique, x1

Pillai (1983); Sheppard & Sheppard (1991).

This species is very distinctive due to its markedly exsert, plocoid, large corallites. Growth form is sub-massive and colonies are up to 50cm in diameter. The color of the living animal is bright green with strikingly white tentacles. Common from northern Natal northwards.

A second species, Galaxea astreata (Lam.), with smaller corallites and a different growth form (submassive to columnar) is only found from Inhaca Island northwards (Plate 19b).

Family Pectiniidae Vaughan & Wells, 1943

Only one genus occurs in South Africa, but in Mozambique two genera of this family occur.

Genus Echinophyllia Klunzinger, 1879

Echinophyllia aspera (Ellis & Solander, 1786) (Plate 20a).

Echinophyllia aspera (Ell.& Sol.); Veron & Pichon (1980); Veron (1986); Sheppard & Sheppard (1991).

Colonies are encrusting to foliaceous, often with a thickened centre. Growth form very variable. Corallites vary from immersed to exsert and almost tubular. Septa and costae strongly dentate. A typical pit to the left and right at the insertion of each new septo-costa differentiates this genus from Oxypora. Common from Natal northwards.

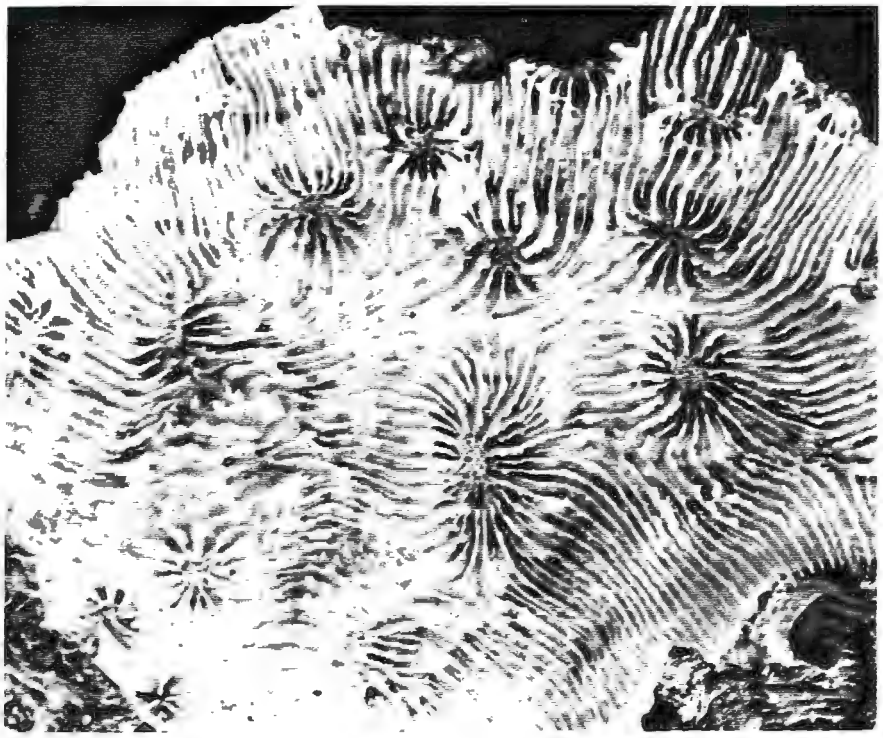


Plate 20a: Echinophyllia aspera, 2-Mile Reef, South Africa, x1.5

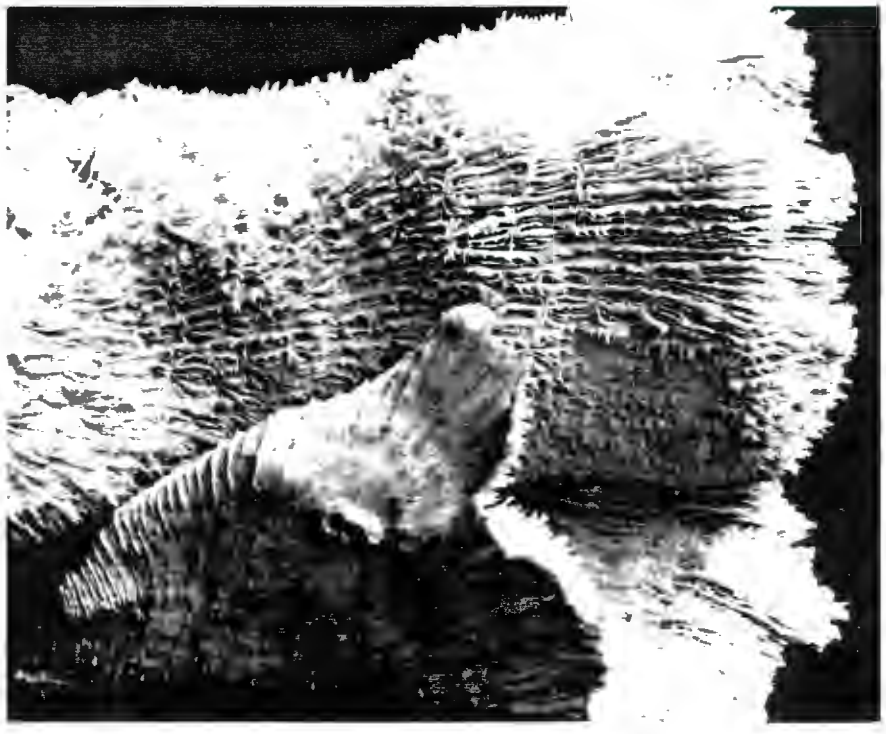


Plate 20b: Oxypora lacera, Inhaca Island, Mozambique, x0.7

Oxypora lacera (Verrill, 1864) is another member of this family, which is present only in Mozambique. It is very similar to Echinophyllia, but lacks the characteristic insertion pits at the origins of new septo-costae (Veron, 1986) (Plate 20b).

Family Mussidae Ortmann, 1890

Members of the family Mussidae are characterized by heavily calcified coralla with thick septa, which are adorned with very big, simple and conspicuous spines. The live animals are often very colourful and in all cases very fleshy.

Genus Blastomussa Wells, 1961

This is a small genus and, physically, the polyps are also the smallest within the Mussidae. The corals are easily identified by the usually incomplete fusion of the corallites.

Blastomussa merleti (Wells, 1961) (Plate 21a)

Blastomussa merleti (Wells); Veron & Pichon (1980); Scheer & Pillai (1983); Veron (1986); Sheppard & Sheppard (1991).

South African colonies are mostly flat and phaceloid to plocoid. A cerioid condition, as reported from Sheppard & Sheppard (1991) from the Red Sea, was not observed in South East Africa. Corallites are around 6mm diameter and often fused in a bead-like manner. Living polyps are often extended by day and have striking colours: red, green or brown or combinations of these colours. Rare in South Africa and Mozambique.

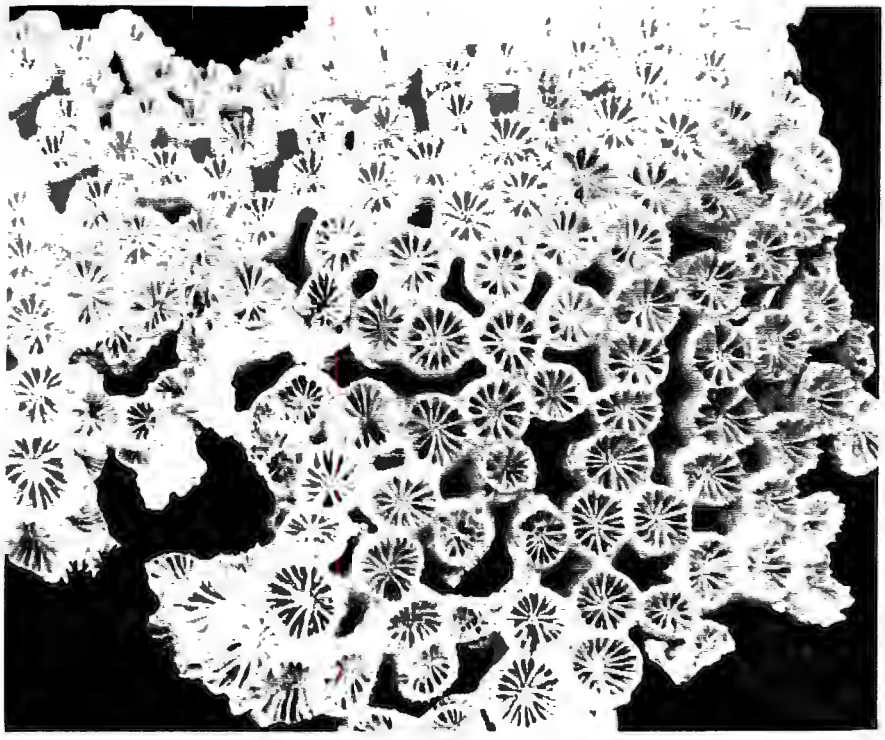


Plate 21a: Blastomussa merleti, 2-Mile Reef, South Africa, x1

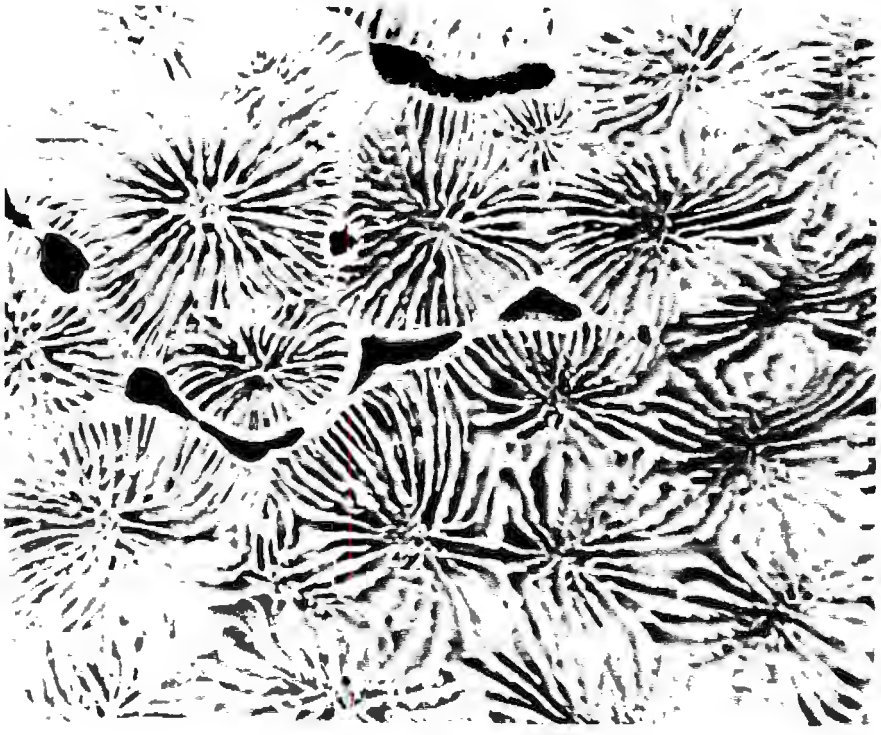


Plate 21b: Acanthastrea echinata, 2-Mile Reef, South Africa, x1

Genus **Acanthastrea** Edwards & Haime, 1848

This is a very common genus on most reefs in the region. It may in some instances be difficult to identify due to similarities to faviid genera such as Favites. However the septal structures of Acanthastrea are typically mussid, being thick and heavily armed with simple spines.

Acanthastrea echinata (Dana, 1846) (Plate 21b)

Acanthastrea echinata (Dana); Veron & Pichon (1980); Scheer & Pillai (1983); Sheppard & Sheppard (1991).

Corals are massive, usually forming flat colonies. Corallites are big (10-20mm) and shallow. Septa are strongly spined as are the costae. In the living animal the spines show through the tissue as concentrical rings around the calyces. There are two colour morphs in the area, red and green. The species is found from the intertidal to the deep subtidal and is everywhere common. It is found from southern Natal and Mozambique northwards.

Acanthastrea simplex (Crossland 1948) (Plate 22a)

Symphyllia simplex Crossland 1948; Boshoff (1981)

?Acanthastrea hillae Wells (1955); Veron & Pichon (1980)

This species is easily separated from A. echinata by the larger size of its corallites (10-40mm). The corallites are cerioid and polygonal. Septa are in two orders, both of which reach the columella and bear regular dentations, the size of which corresponds to the size of the septa. All septa are exsert and those of adjacent corallites join. Colonies are usually small, consisting only of a few corallites. This species is certainly close to A.maxima Sheppard & Salm, but is differentiated by

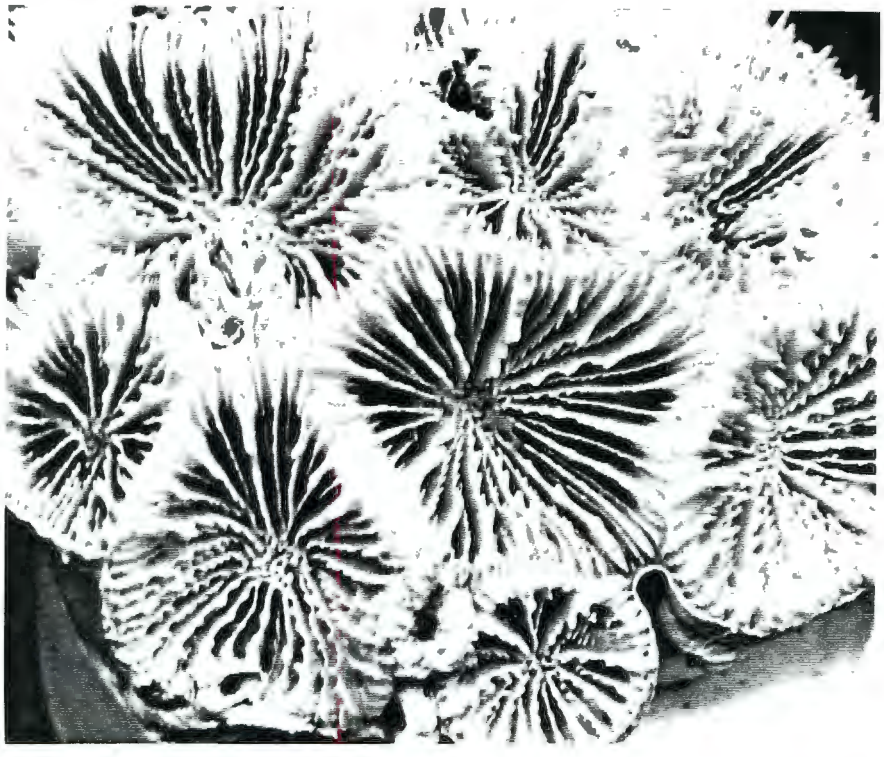


Plate 22a: Acanthastrea simplex, Inhaca Island, Mozambique, x1.7

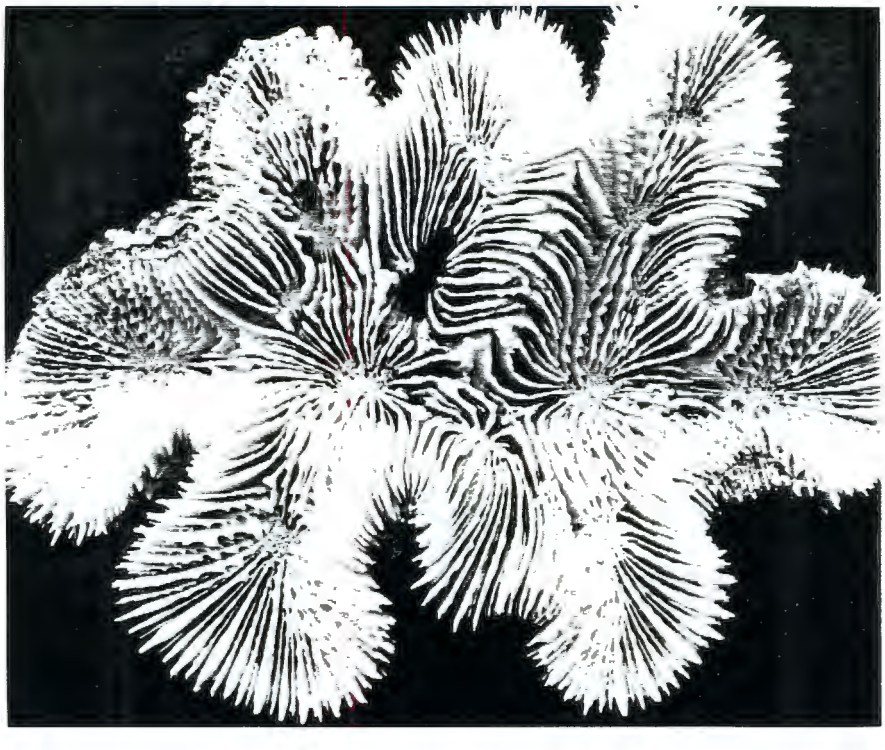


Plate 22b: Symphyllia valenciennesi, 4-Mile Reef, South Africa, x0.4

smaller corallites and septal dentations. It is also close, possible synonymous with A. hillae Wells, but more material is needed to confirm this assumption.

Genus **Symphyllia** Edwards & Haime, 1848

Only one species occurs in our region and is quite common. This genus is easily recognized by its very big, meandroid corallites.

Symphyllia valenciennesi Edwards & Haime, 1849 (Plate 22b)

Symphyllia valenciennesi Ed.& H.; Veron & Pichon (1980); Veron (1990).

This species is easily identified by its large (around 5cm), meandroid corallites. Colonies are never big, achieving a diameter of up to 30cm. The living animal is often vividly coloured, with bright centres. Colours vary from red to green. The species is common on the deeper reefs. South Africa and Mozambique.

Genus **Lobophyllia** Blainville, 1830

There are two species, **L. corymbosa** (Forskal) (Plate, 23a) and **L. hemprichi** (Ehrenberg), which only occur from Mozambique north, but are absent in South Africa. Corallites in L. corymbosa are smaller than in A. hemprichi and never reach a similar degree of meandrisation. L. corymbosa hardly exceeds a tristomodeal stage, while L. hemprichi often forms long meanders. The individual corallites (or series of corallites) are often not attached to each other, which may lead to colonies falling apart and forming only a more or less chaotic heap of corallites.

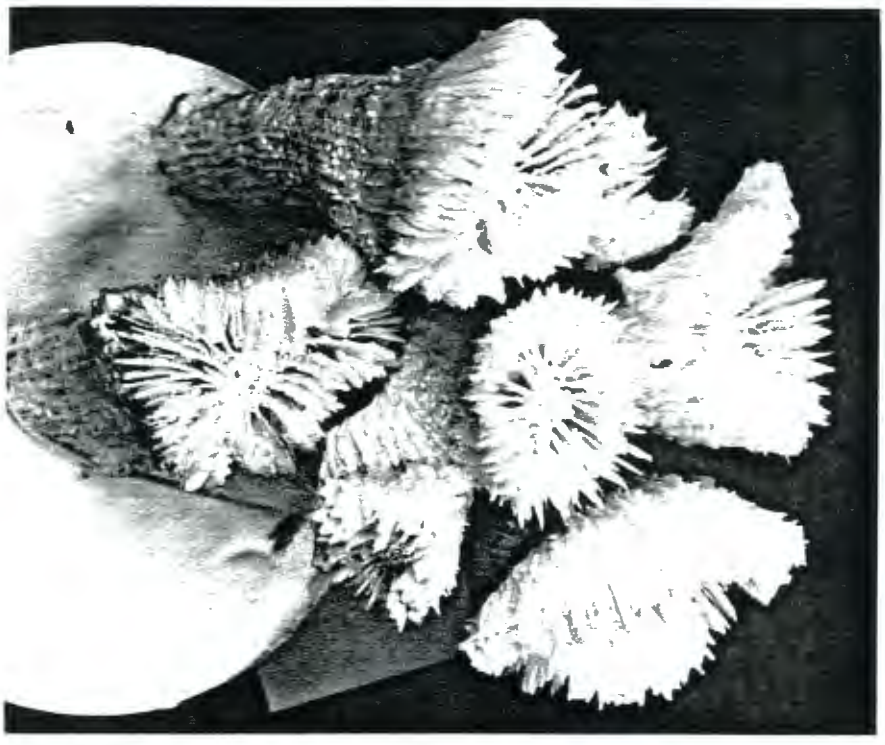


Plate 23a: Lobophyllia corymbosa, Inhaca Island, Mozambique, x0.5

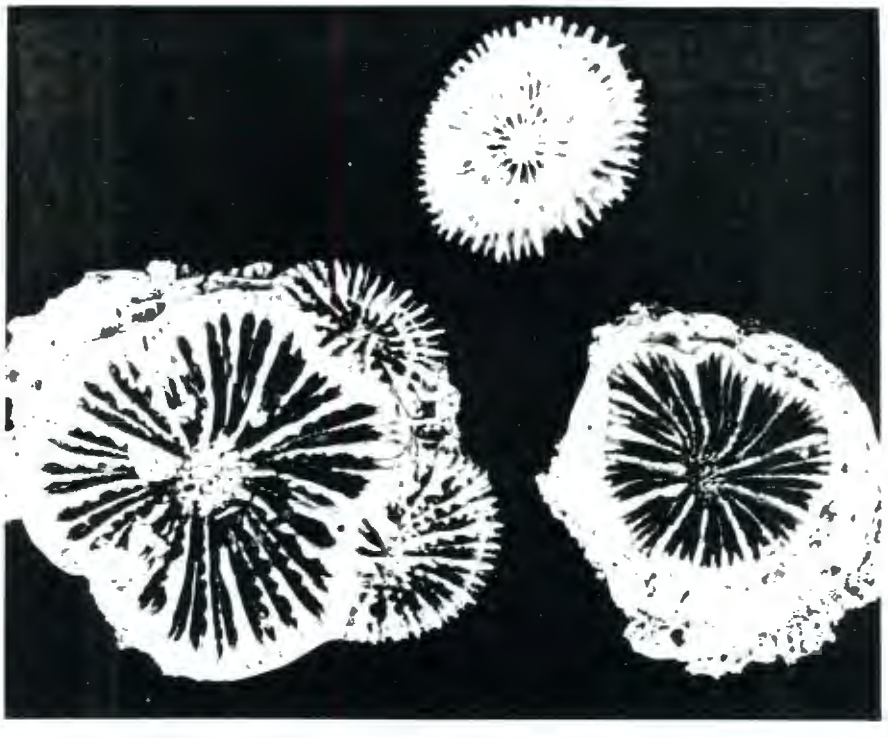


Plate 23b: Scolymia cf. vitiensis, 9-Mile Reef, South Africa, x1

Genus **Scolymia** Haime, 1852

This is one of the few solitary, but attached hermatypic corals. It is easily identified by the large, solitary polyps.

Scolymia cf. vitiensis Brueggemann, 1877 (Plate 23b)

Scolymia vitiensis Bruegg.; Veron & Pichon (1980); Veron (1986).

The corallum is a solitary corallite, disc-shaped, about 5cm in diameter. Extratentacular budding often produces one or two small daughter colonies attached to the side of the bigger corallum. Colour is usually a vivid green. Common but often overlooked. So far recorded from southern Natal (Aliwal Shoal) northwards.

Family **Merulinidae** Verrill, 1866

One genus occurs in South Africa, a second one is only found from Mozambique northwards.

Genus **Hydnophora** Fisher de Waldheim, 1807

This genus is unique in its possession of hydnophoroid corallites. Only parts of the thecae are raised and, together with attendant septa,form the so called "hydnae", which gave the genus its name. This genus used to be considered as belonging to the Faviidae until Veron (1986) grouped it with the Merulinidae, where it has remained so far (Veron & Marsh, 1988; Sheppard & Sheppard, 1991).

Hydnophora exesa (Pallas, 1766)

Hydnophora exesa (Pallas); Veron et al. (1977); Scheer & Pillai (1983); Veron (1986); Sheppard & Sheppard (1991).

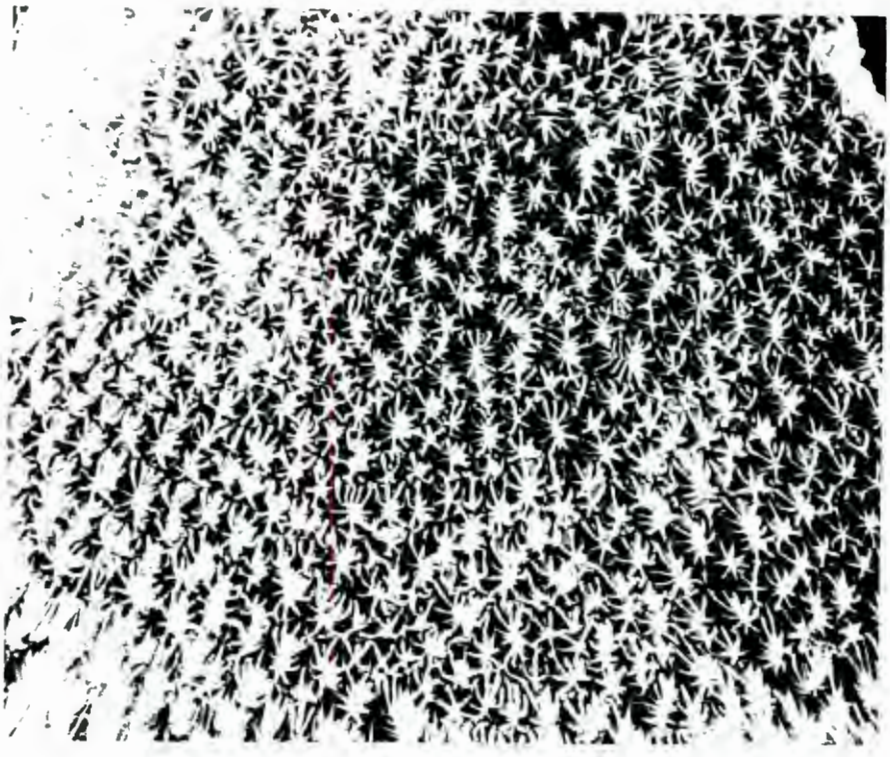


Plate 24a: Hydnophora microconos, 9-Mile Reef,South Africa, x1

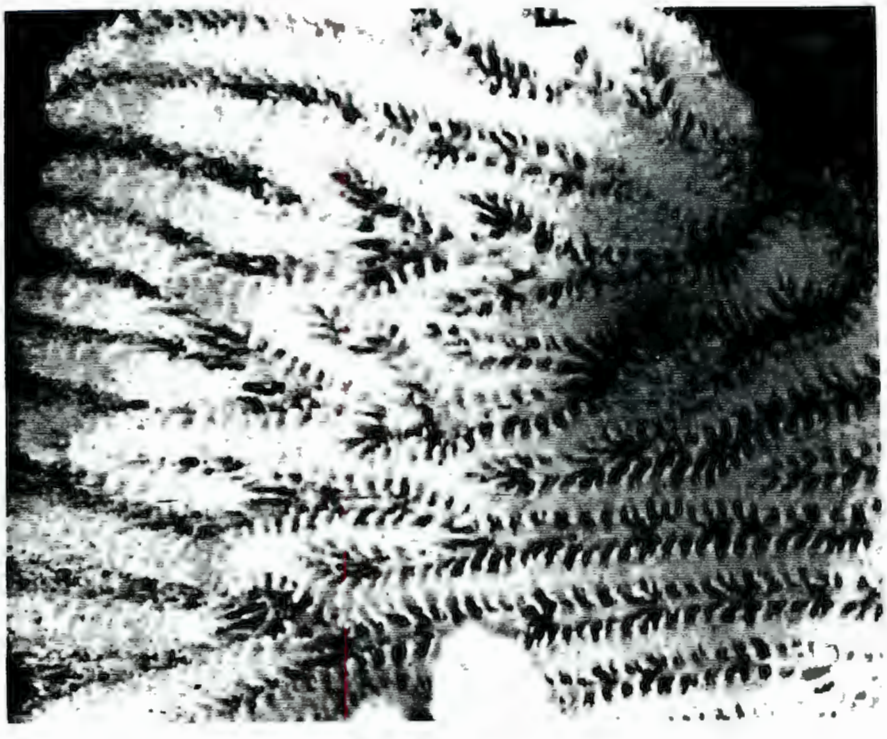


Plate 24b: Merulina ampliata, Inhaca Island, Mozambique, x1.5

Large hydnae (3-4mm diameter), which fuse to form ridges. Septa mostly in one order, but sometimes a second order is present. Septa are dentate. Growth form is massive to ramose. Common from northern Natal northwards.

Hydnophora microconos (Lamarck, 1816) (Plate 24a)

Hydnophora microconos (Lam.); Veron et al. (1977); Scheer & Pillai (1983); Veron (1986); Sheppard & Sheppard (1991).

Smaller hydnae (2-3mm diameter), which do not fuse to form ridges. Septa in two orders. Second order septa do not reach the top of the hydnae; first order septa are flattened at the top, giving a star-shaped appearance. Growth form massive to columnar. Less common than the previous species. From northern Natal northwards.

Another species in this family Merulina ampliata (Ell. & Sol., 1786) occurs only in Mozambique. It is easily identified by long valleys (Plate 24b) and a lamellar, often contorted growth form.

Family **Faviidae** Gregory, 1900

This important and big family is treated in greater detail in Part I, Chapter 3. It is represented in South Africa and Mozambique by the following species:

Favia favus, F. pallida, F. speciosa, F. laxa, F. matthai, F. rotumana, F. stelligera; Favites pentagona, F. abdita, F. complanata, F. peresi, F. flexuosa, F. halicora; Goniastrea pectinata, G. retiformis, G. edwardsi; Platygyra daedalea; Oulophyllia crispa; Leptastrea purpurea; Cyphastrea chalcidicum;

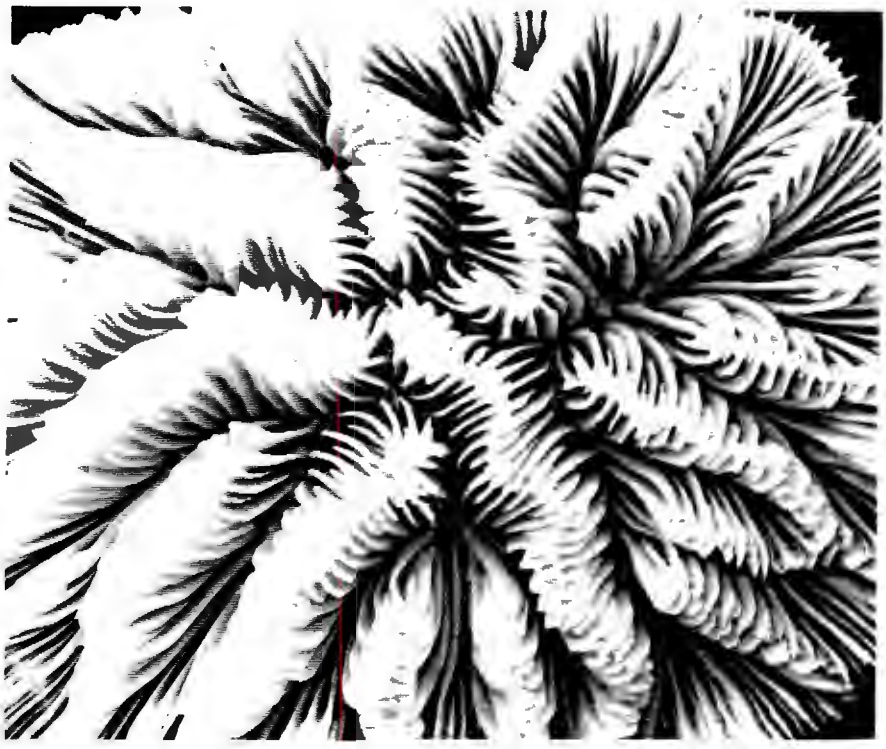


Plate 25a: Gyrosmilia interrupta, 9-Mile Reef,South Africa, x2

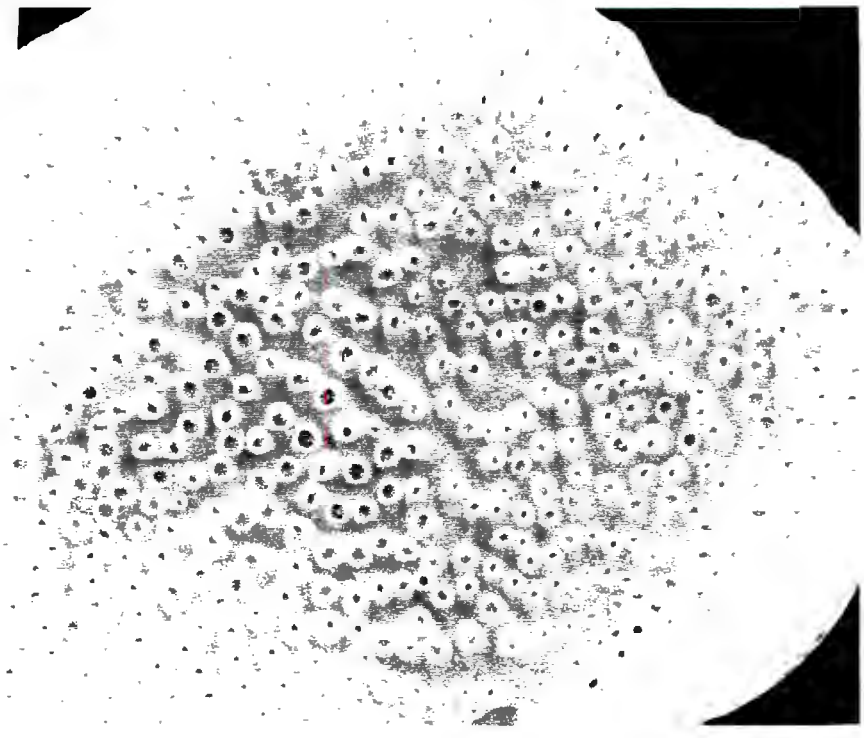


Plate 25b: Turbinaria mesenterina, Inhaca Island, Mozambique, x0.5

Echinopora gemmacea, E. hirsutissima; Montastrea annuligera; Plesiastrea versipora.

The following species are only found in Mozambique: Leptoria phrygia; Echinopora lamellosa; Leptastrea bottae; Montastrea curta.

Family Caryophylliidae Gray, 1847

This a family of mostly ahermatypic corals, only one of six subfamilies being hermatypic (Veron, 1986).

Genus Gyrosmilia Edwards & Haime, 1851

Gyrosmilia interrupta (Ehrenberg, 1834) (Plate 25a)

Gyrosmilia interrupta (Ehrbg.); Scheer & Pillai (1983); Veron (1986); Sheppard & Sheppard (1991).

Colonies are massive, typically hemispherical and reach diameters up to 40cm. Valleys are long and centres are not separated. Septa from adjacent valleys do not fuse, but a fine intercalicular groove is maintained. Septal edges and sides are smooth. No columella. The colour of the living animal is chocolate brown to brown with a greenish hue. This species is common in northern Natal and Mozambique.

Family **Dendrophylliidae** Gray, 1847

This large family includes both zooxanthellate hermatypic genera and azooxanthellate ahermatypic genera. The latter are common all around South Africa, not being confined to tropical waters. The

former occur only in the warm waters of northen Natal and Mozambique.

Genus **Turbinaria** Oken, 1815

This is a widely distributed and common genus. It is common in high latitudes in Australia and Africa (Veron, 1986).

Turbinaria mesenterina (Lamarck, 1816) (Plate 25b)

Turbinaria mesenterina (Lam.); Veron & Pichon (1980); Veron (1986); Sheppard & Sheppard (1991).

Colonies are typically vasiform plates, in extreme cases flat plates, with a diameter of up to 1.5m. Corallites are exsert, large (3mm calyx diameter). The colour of the living animal is brown but the growing edge is often white.

Genus **Tubastraea** Lesson, 1829

There is only one species in this genus, which can be considered hermatypic (Schuhmacher, 1984). It is distinguished from the genus Dendrophyllia, which is very similar, by the fact that only in young corallites do septa fuse according to the Pourtales plan (Veron, 1986).

Tubastraea micranthus (Ehrenberg, 1834) (Plate 26a)

Tubastraea micranthus (Ehrbg.); Scheer & Pillai (1983); Schuhmacher (1984); Veron (1986); Sheppard & Sheppard (1991).

Colonies are dendroid and up to 1m tall. Corallites are large, about 1cm in diameter and well exsert. Without zooxanthellae,

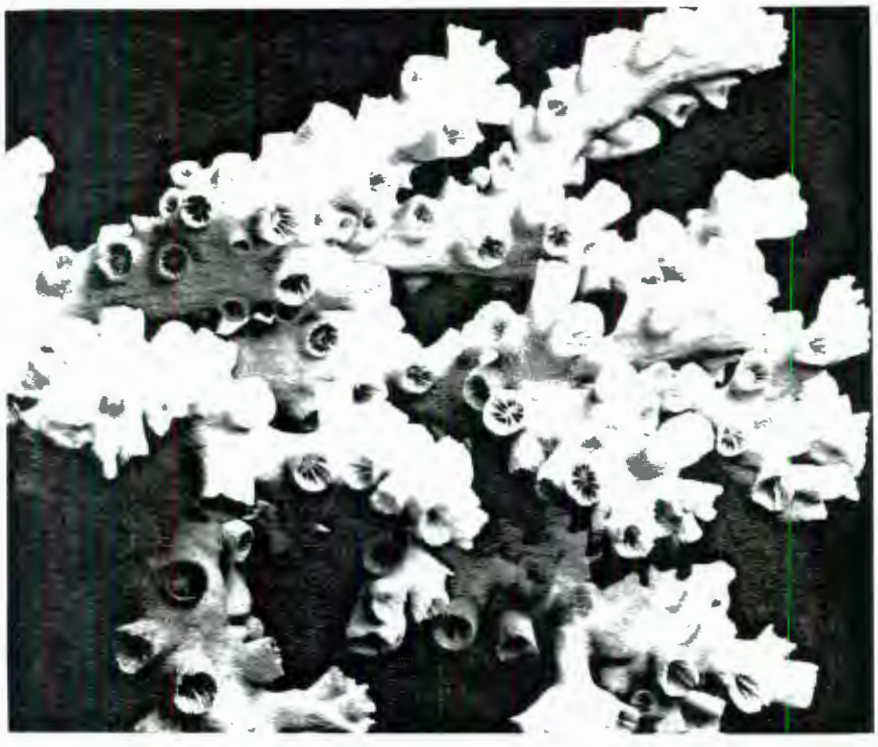


Plate 26a: Tubastraea micranthus, Inhaca Island, Mozambique, x0.25

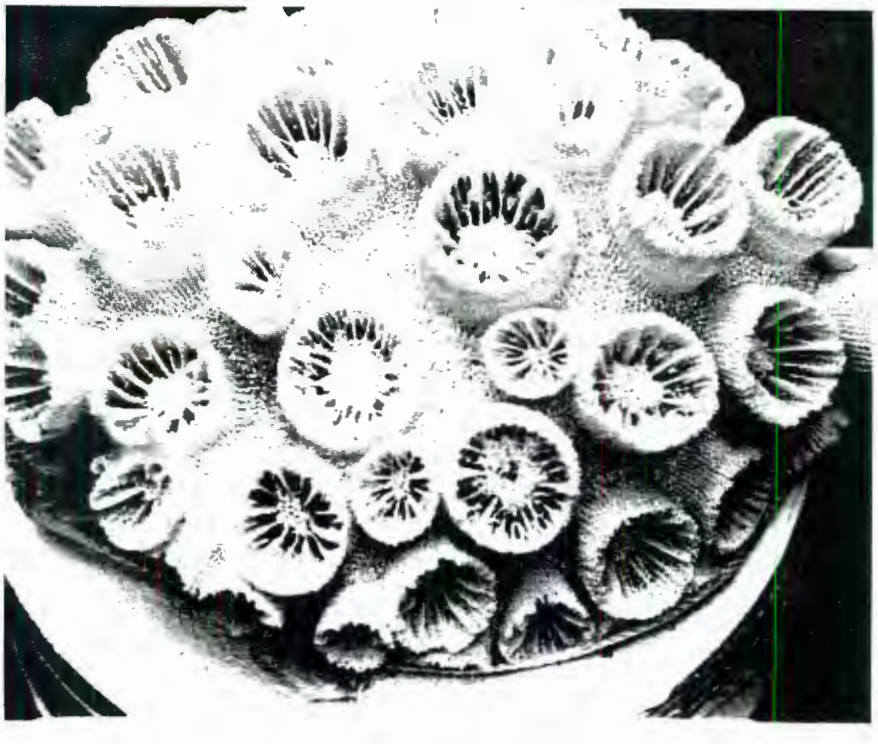


Plate 26b: Dendrophyllia cf. robusta, Inhaca Island, Mozambique, x2

colour of the living animal is green to black. Typically only found in deep areas. Rare in South Africa and Mozambique.

Genus **Dendrophyllia** Blainville, 1830

This is an essentially ahermatypic genus, which is however found very frequently on reefs. Therefore it is included in this chapter. Differences between it and the genus Tubastraea are discussed above.

Dendrophyllia cf. robusta Bourne, 1905 (Plate 26b)

Dendrophyllia robusta Bourne; Scheer & Pillai (1983); Sheppard & Sheppard (1991).

The colonies are usually low clumps, with very large corallites. The pattern of septal fusion following the Pourtales plan is clearly visible in mature polyps. Living colonies are often brightly colored.

Discussion

The 90 species found in South Africa and the 115 found in subtropical Mozambique are mostly of wide Indo-Pacific distribution. Most of them are new records, at least for South Africa, as no detailed study on this area has yet been published. Records from Mozambique in Boshoff (1981) are dubious, as most of them are misidentifications or invalid synonyms were used.

Subtropical South East Africa has a very rich coral fauna, which is comparable to other faunas in the western Indian Ocean (Sheppard, 1987), but it seems to be poorer than the eastern Indian Ocean fauna.

In this study more species of coral were found in subtropical southern Mozambique (115) than have been recorded from tropical East Africa (112 in Sheppard, 1987). This is comparable to a similar increase in species richness in the Northern Red Sea (134 in Sheppard, 1987). It is hard to believe that peripheral, subtropical areas should be richer in species than the tropical centre. I therefore believe that the relative paucity of species in tropical East Africa merely reflects a lack of research rather than an actual lack of diversity.

The hermatypic coral species richness in South Africa declines very steeply from northern Natal, where 90 species are present, to central Natal, where only about 10 species can be found. Aliwal Shoal, which provides roughly the same habitats as the Maputaland Reef Complexes in northern Natal, does not harbour any reef coral communities, but only isolated colonies of about 10 species. It is possible, that the lack of any suitable substratum over more than 500km coupled with freshwater and silt input by the Umfolozi, the Tugela and numerous other rivers form a barrier not allowing the majority of species spreading into central and southern Natal. Along the Transkei coast only about 5 species of hermatypic corals are found. This number declines further in the Eastern Cape, where only one species, Stylophora pistillata, is occasionally found as far south as Port Elizabeth (Day, 1969).

A REVISION OF THE HARD CORAL GENUS ACROPORA Oken, 1815 (Scleractinia: Astrocoeniina: Acroporidae) IN SOUTH-EAST AFRICA

Abstract

In this monograph all species of the scleractinian coral genus Acropora presently known to occur in South East Africa (denoting the African coast south of the Tropic of Capricorn, and including the Atoll Bassas da India in the Mozambique channel) are reviewed. Twenty three species are discussed, most of whichs are of wide Indo-Pacific distribution. Field and laboratory characteristics of all species are described in detail. Species richness in southern Mozambique is much higher (23 species) than in South Africa (14 species), probably due to the higher ecological differentiation of Mozambiquan reefs. The Acropora fauna of the Atoll Bassas da India is similar to that found in Mozambique but with two species A. paniculata and A. cf. striata, which have not yet been found on the African mainland coast. Compared to other reefal areas in similar latitude, the South East African Acropora fauna is of average diversity.

Introduction

The genus Acropora is the biggest scleractinian genus with no less than 364 nominal extant species (Veron & Wallace, 1984). Over most of the Indo-Pacific it is one of the most common and ecologically important genera to occur in coral communities (Wallace, 1978). The South East African coast, from the Tropic of Capricorn in the north to Transkei in the south, constitutes the extreme western and southern boundary for Indo-Pacific Acropora and therefore merits special attention. This area also experiences the transition from tropical to sub-tropical conditions, and it is of great biogeographical interest. Only one species, Acropora africana (Brook, 1893, type locality: South Africa, "Cape of Good Hope") has so far been described from the South East African coast and the whole region has largely been neglected in systematic coral research.

However, extensive coral communities occur in Mozambique and in northern Natal in South Africa, wherein Acropora species are important community members.

South East Africa, being situated in the extreme west of the Indian Ocean faunal province, forms a cul-de-sac for species arriving at its shores as no currents, which would provide transport for larvae, lead immediately back into warm waters. However, a one-way transport exists for larvae or rafting adults in the headwaters of the forming Agulhas current, moving southwards in the Mozambique channel. Theoretically, the South East African species would have arrived either by moving down the coast from tropical East Africa or by being carried over from

Madagascar via Bassas da India and Europa Island by the current. This isolation is a situation favouring the development of local, peripheral endemism (Rosen, 1988).

This chapter investigates the Acropora fauna of Southern Mozambique, South Africa and, to a very limited extent, of the Atoll Bassas da India in the Mozambique channel between Mozambique and Madagascar, with a view to increasing the understanding of the biogeography of this genus.

Material and Methods

Collecting was done to a very detailed level along the South-East African coast (Fig. 1). Collecting sites were on Inhaca Island, off Maputo in southern Mozambique, and on The Northern. Central and Southern Reef Complexes in northern Natal, where extensive coral communities occur (Boshoff, 1980, 1981). A casual collection was brought back from Bassas da India by two expeditions launched by the Oceanographic Research Institute in Durban.

In the 1950's and 60's a large collection of corals was gathered by Dr. P. Boshoff mainly from Inhaca Island and the coast of southern Mozambique (Fig.3). His collection and publications (Boshoff, 1980, 1981) are reviewed here to provide up-to-date taxonomic information about Acropora in southern Mozambique.

In South Africa large coral assemblages occur on submerged fossil dune systems along the Maputaland coast (Boshoff, 1980, 1981; Ramsey and Mason, 1990). These reefs form the southernmost limit where Acropora occur in any important numbers in Africa. These

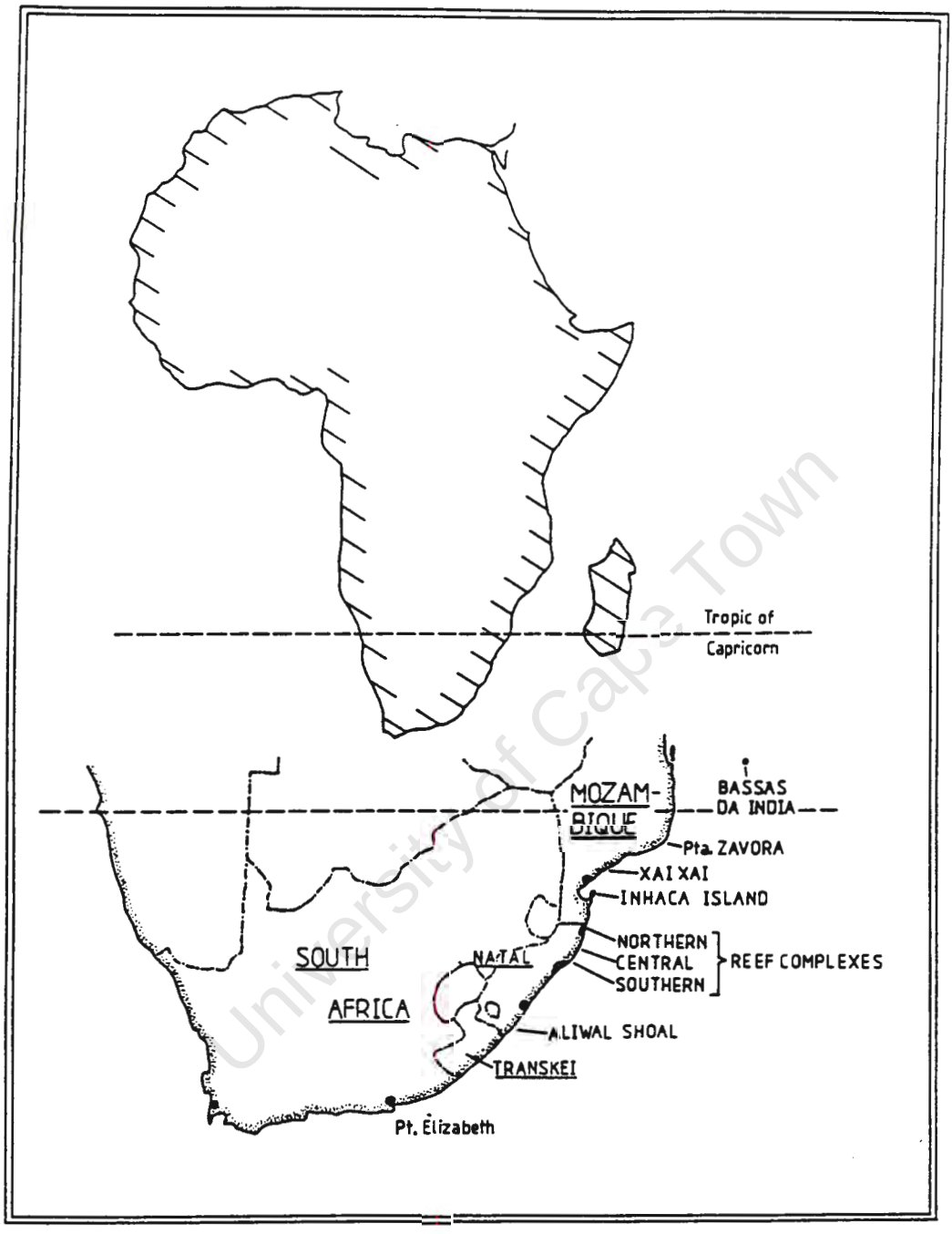


Fig. 1: Overview of South East Africa showing the overall geographical setting of sample locations along the South African and Mozambiquan coast, as well as the Atoll Bassas da India in the Mozambique channel.

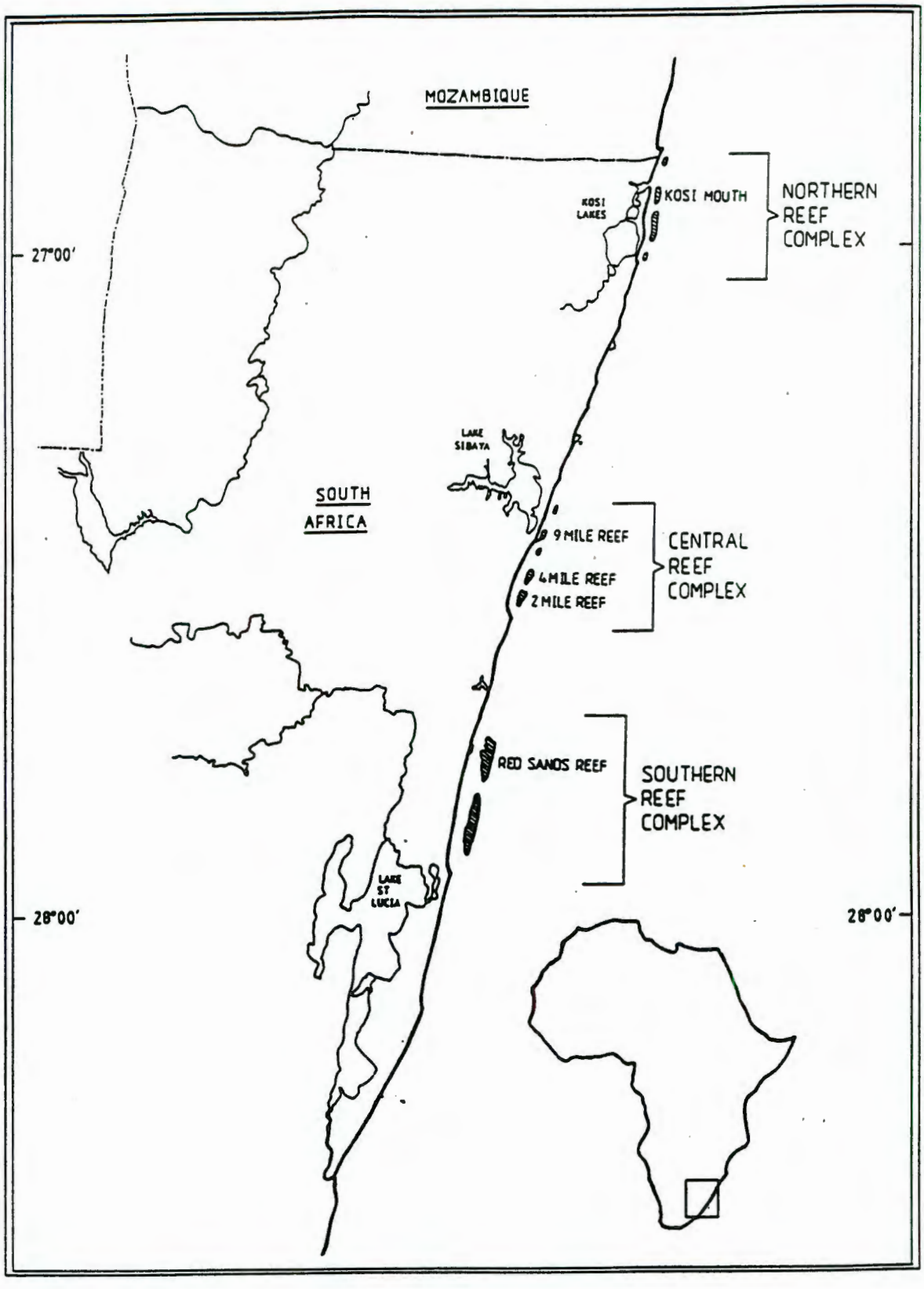


Fig. 2: The reef system off the Maputaland coast in northern Natal, RSA. Coral communities grow on fossilized dunes parallel to the coast. Only reefs, on which collecting for the present publication was done have their names given.

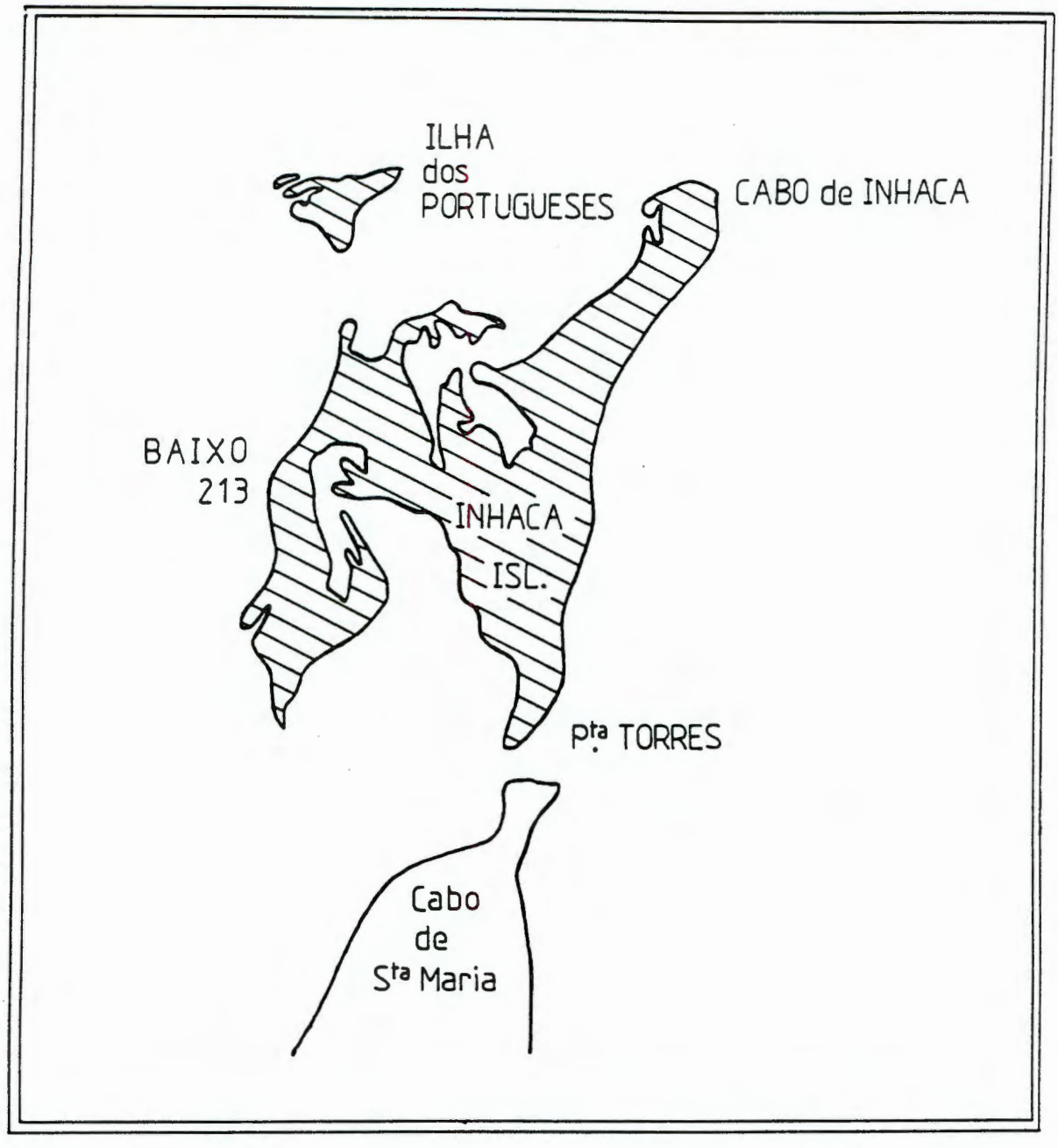


Fig. 3: The sampling sites on Inhaca Island, Mozambique.

reef systems were extensively sampled for the present publication (Fig.2).

Collecting stations

Collecting in South Africa was done on all major reef systems. Collecting stations were (Fig.2):

In the Northern Reef complex (Kosi Bay):

off Kosi Mouth (20-24m); 26°45'S; 32°44'E.

In the Central Reef complex (Sodwana Bay):

2-Mile Reef (7-36m); 27°31'S; 32°41'E.

4-Mile Reef (18-24m); 27°29'S; 32°41'E.

9-Mile Reef (6-20m); 27°25'S; 32°42'E.

In the Southern Reef comlex:

Red Sands Reef (10-40m); 27°45'S; 32°38'E.

Collecting in Mozambique was done by Dr. P. Boshoff (Boshoff, 1981) mainly at Inhaca Island and various localities along the southern Mozambiquan coast north to Inhambane (Fig.1). The most important areas were (Fig. 3):

On Inhaca Island (26°10'S; 32°30'E):

Cabo de Inhaca (rock pools and open sea)

Ilha dos Portugueses (pools and lagoons)

Baixo 213 (reef)

Pta. Torres (reef)

On the mainland:

San Martinho, close to Xai Xai (small lagoons); 25°19'S; 33°30'E.

Xai Xai (small lagoons); 25°08'S; 33°30'E.

Ponta Zavora (small lagoons); 24°21'S; 25°12'E.

Also a casual collection of corals was brough back from Bassas da India by two expeditions staged by the Oceanographic Research Institute. As this Atoll lies halfway between Mozambique and Madagascar (Fig. 1) it is of biogeographical significance. The Acropora from this collection, which were taken from the lagoon, are included in the present paper.

Taxonomic notes

The Indo-Pacific members of the genus Acropora have received exhaustive revision by Wallace (1978) and Veron and Wallace (1984). Thanks to these publications the taxonomic situation in Acropora has been stabilized and it is now possible to use these recent publications as references (Veron & Marsh, 1988, Sheppard, 1991). I have therefore refrained from embarking on a total revision of type material where this has already been done by the above-mentioned authors. Also, I have only given short synonymy lists, based on the literature pertinent for the area under investigation and only purely taxonomic paper are listed. The complete synonymy lists are to be found in Veron and Wallace (1984). I have adopted most of the taxonomic views and interpretations of Veron & Wallace (1984) as taxonomic stability is badly needed in this large genus.

Abbreviations

The following abbreviations were used in the text:

-for institutions: ORI Oceanographic Research Institute, Durban, South Africa

SAM South African Museum, Cape Town, RSA.

-for morphology: R fraction of a corallites radius to which septa extend (e.g. 1/4 R, septa are developed along one quarter of the corallite's radius).

Characters and Terminology

In this chapter the same terminology is used as in Wallace (1978) and Veron and Wallace (1984), where Acropora morphology is exhaustively described. Therefore only a short description of the technical terms used in this chapter is given (Fig.4).

Generic characteristics

The genus Acropora, with its two subgenera Acropora and Isopora, is primarily characterized by its highly organized growth form, which results from a differentiation of polyps, and therefore corallites, into axials and radials. Within the subgenus Acropora, which is by far the bigger of the two, the axial corallites are usually larger than the rest and decide the direction and orientation of branch growth. The radial corallites are given off by the axials and are responsible for the lateral growth of the branches, creating their thickness. Within the subgenus Isopora, which is the smaller, consisting only of three species, no clear differentiation of any one single axial corallite is observed, but

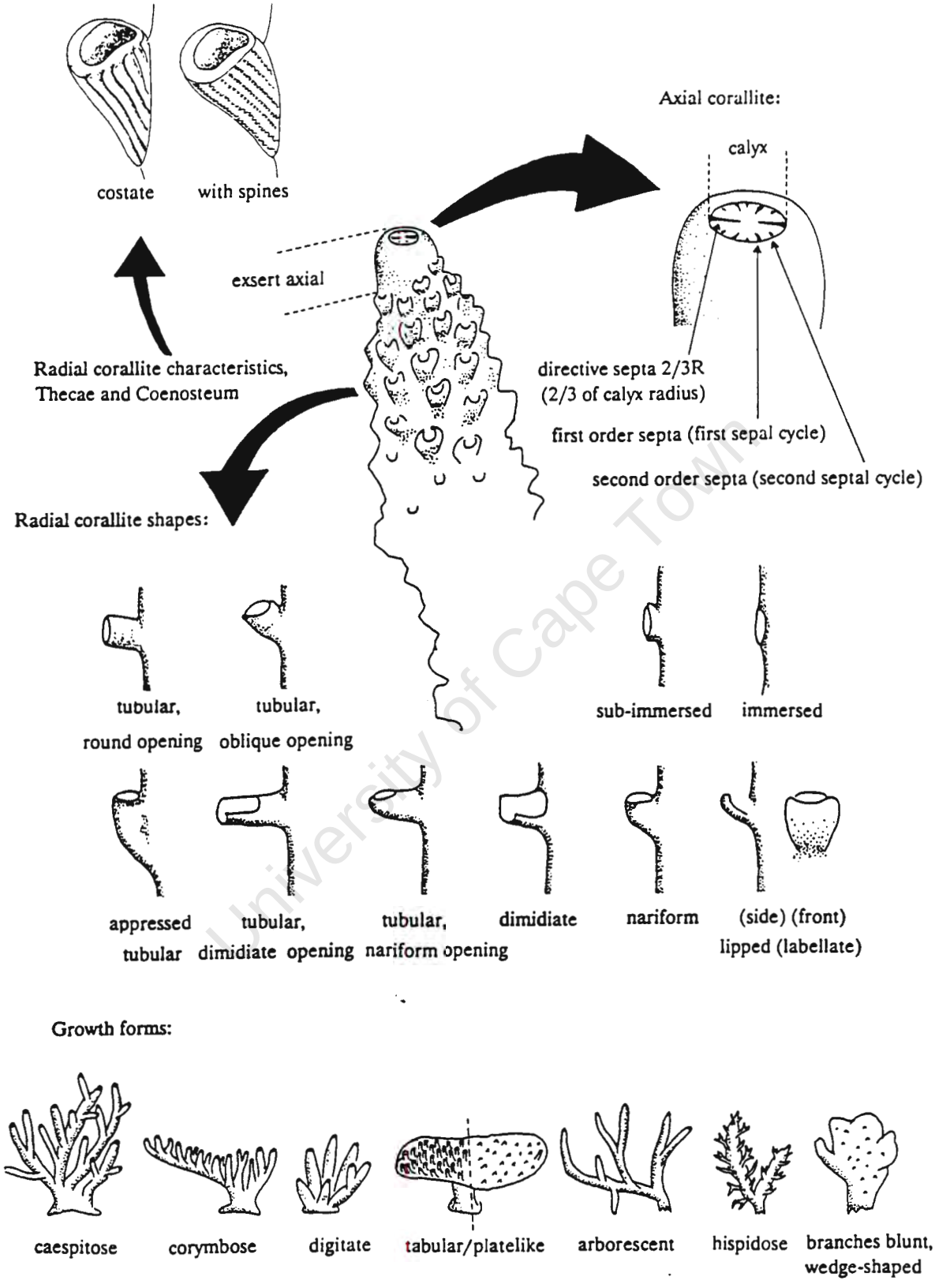


Fig. 4: Illustration of technical terms used for Acropora morphology in the present publication. Partly redrawn from Wallace (1978) and Veron & Wallace (1984).

a number of equivalent axials determine the direction of growth. Therefore the branches developed by this subgenus are much thicker and blunter than those in the subgenus Acropora. In extreme cases no axial corallites are developed at all and all corallites are equivalent, which causes the whole corallum to have a massive growth form.

This differentiation of corallites allows this genus to be very variable in its growth form, even at a species level. Growth form can be greatly modified according to environmental conditions. Within this ability rests most probably the secret of this genus's success on reefs all over the world.

SUBGENUS ISOPORA Studer, 1878

ACROPORA (ISOPORA) PALIFERA (Lamarck, 1816)

(Plate 1a)

Synonymy:

Astrea palifera Lamarck, 1816.

Madrepora palifera (Lamarck); Brook (1893).

Madrepora labrosa Dana, 1846; Edwards & Haime (1860); Verrill (1902).

Isopora labrosa (Dana); Studer (1878).

Madrepora palifera (Lamarck); Brook (1893); Verrill (1902).

Acropora palifera (Lamarck); Scheer & Pillai (1974); Pillai & Scheer (1976), Veron & Marsh (1988), Veron (1990).

Acropora (Isopora) palifera (Lamarck); Veron & Wallace

(1984), Veron (1986).

Material examined: 4 specimens from Bassas da India (ORI/BdI/1991-8-7, ORI/BdI/1991-8-9, ORI/BdI/1991-8-45, ORI/BdI/1991-8-46), 6 fragments from 2 colonies from the Northern Reef Complex, RSA (ORI/KB/1991-9-10, 1991-9-11, 1991-9-12, 1991-9-13).

Branching pattern:

Very blunt, wide branches, taking the form of lobes, with no clear differentiation of a single axial corallite. Branches are given off in all directions, vertically and horizontally. Colonies may also be massive, with no branches at all, or encrusting.

Axial corallites:

Similar in size and shape to the radials, although sometimes either larger or smaller. They can be recognized by being surrounded by radials in form of a rosette (ORI/BdI/1991-8-45). This situation occurs most frequently on the growing edge, but also on incipient axial corallites along the sides of branches or plates. **Septation:** as in radial corallites.

Radial corallites:

More or less uniform in size; tubular to tubular appressed with round to elongate opening; individual corallites with nariform opening. The lower wall is often thickened. Orientation of corallites is not uniform. **Septation:** well developed in most corallites with two cycles, which may be complete or incomplete with a reduced second cycle. The directive septa are often prominent (first cycle 1/4-1/2R, directives 1/2-3/4R, second cycle 1/8-1/4R).

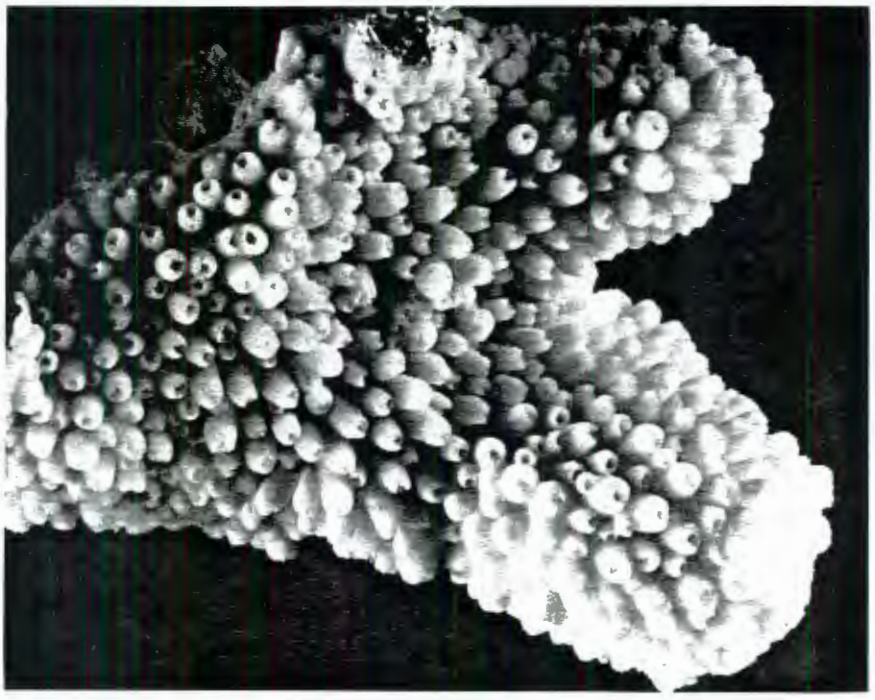


Plate 1a) Acropora (Isopora) palifera (Dana, 1846); ORI/BdI/1991-8-7, x1, from Bassas da India, Lagoon.

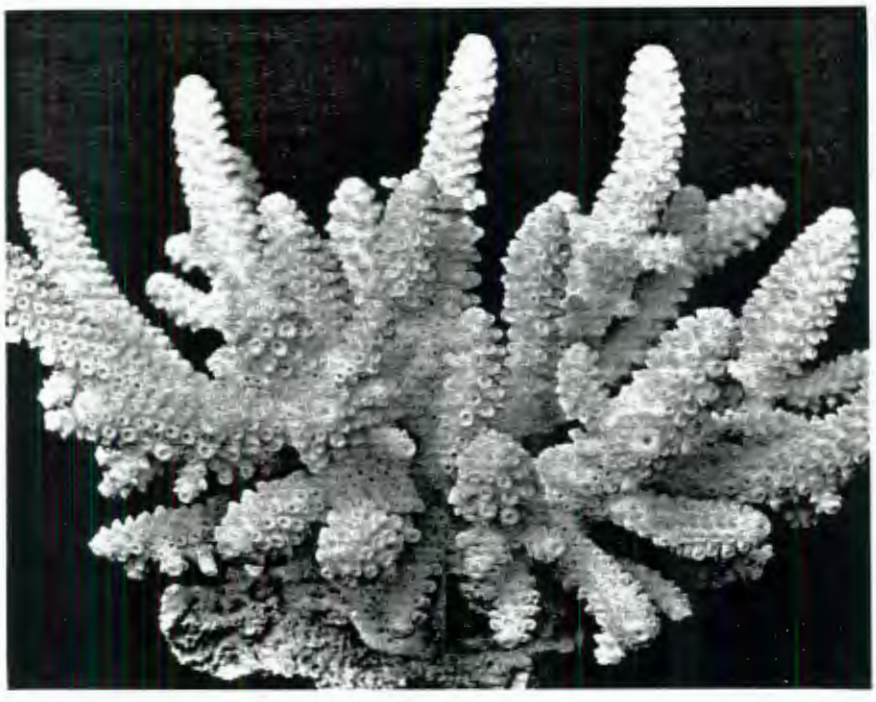


Plate 1b) Acropora (Acropora) humilis (Dana, 1846); ORI/S2/2-9-10/2, x0.7, from 2-Mile Reef, Central Reef Complex, Natal, RSA.

Thecae and Coenosteum:

An equal arrangement of strong spines with elaborate tips. The spines may anastomize.

Observations:

This species is very variable in its growth form. The specimens from Bassas da India were collected in the lagoon and represent an ecomorph from a protected, well-lit biotope and have relatively long branches and moderate calcification. The specimens from the Northern Reef Complex are fragments from two massive, hemispherical colonies, which were growing at 20 and 21 metres depth respectively. These colonies were almost completely round and had only a few humps instead of branches. The specimens ORI/KB/1991-9-10 and ORI/KB/1991-9-13 are these humps. Another frequent growth form in the Northern Reef Complex is flat encrusting. This species has not yet been recorded from reefs further south (i.e. the Central and Southern Reef Complexes).

SUBGENUS ACROPORA Veron & Wallace, 1984

The Acropora humilis group:

The following four species have been grouped by Veron and Wallace (1984) as belonging to the Acropora humilis group; being "...all similar heavy-structured species with thick branches and a corymbose growth form...". The species are easily identified by their usually stout, straight branches with prominent axial corallites and radials often neatly arranged in rows or spirals. Colonies mostly have a low, pillow-like appearance.

ACROPORA (ACROPORA) HUMILIS (Dana, 1846)

(Plate 1b)

Synonymy:

Madrepora humilis Dana, 1846; Brook (1893)

Acropora humilis (Dana); Scheer & Pillai (1974), Pillai & Scheer (1976), Wallace (1978), Scheer & Pillai (1983), Veron & Marsh (1988), Sheppard & Sheppard (1991).

Acropora (Acropora) humilis (Dana); Veron & Wallace (1984), Veron (1986),

Material examined:

1 specimen from 2-Mile Reef, Central Reef Complex, RSA (ORI/S2/2-9-10/2), 1 specimen from Inhaca Island, Mozambique (ORI/AIC17(2) from Pta. Torres).

Branching pattern:

Caespito-corymbose from a central attachment. Branches thick (diameter 8.3 - 10.9mm), slightly tapering. Not all branches are the same length, numerous branchlets being given off on the lower part of the main branches.

Axial corallites:

Moderately exsert (1.5 to 2.4mm), very large and conspicuous (outer diameter 3.5 - 4.4mm, calyx diameter 1.3 - 2mm). **Septa:** in 2 complete cycles (first cycle 1/4 - 1/2R, second cycle about 1/4R); when first cycle septa are small, then directive septa are prominent.

Radial corallites:

Tubular, usually with elongate opening, spreading at about 90

degrees from the main branch. Often arranged in rows or spirals. Small subimmersed corallites are interspersed on the lower part of the branches. Numerous incipient axials are present, which frequently develop into branchlets. **Septa:** reduced in ORI/S2/2-9-10/2 to a row of spines in most corallites, only one cycle, often only one directive septum well developed with a few other septa developed only as small ridges. In ORI/AIC17(2) two complete cycles are present in a few corallites (first cycle 1/3, second cycle 1/4R), most corallites however only with one cycle.

Thecae and Coenosteum:

Reticulate with laterally flattened spines. The spines often fuse to form costae on the corallites.

Observations:

The specimen from South Africa is a typical deep water specimen with long, irregular branches and many incipient axials. This species is rare in South Africa.

ACROPORA (ACROPORA) GEMMIFERA (Brook, 1892)

(Plate 2a)

Synonymy:

Madrepora gemmifera Brook, 1892; Brook (1893).

Acropora gemmifera (Brook); Veron & Marsh (1988).

Aropora (Acropora) gemmifera (Brook); Veron & Wallace (1984), Veron (1986).

Material examined:

2 specimens from Inhaca Island, Mozambique (ORI/AIC1(1) from Baixo 213, ORI/AIC4(1) from Pta. Rasa); 1 specimen from Pta. Zavora,

Mozambique coast (ORI/AICII(2)).

Branching pattern:

Corymbose, the originally encrusting base may grow massive as the corallum increases in size, growing upwards and fusing the basal part of the branches together (as seen in ORI/AICII(1)). Branches are thick and terete for most of their length, only tapering at the tip.

Axial corallites:

Hardly exsert (1-1.7mm), conical with thick walls, tapering from a basal diameter of 3-4mm to 2.8-3.8mm distal diameter, calyx diameter 0.7-1mm. **Septa:** two well-developed, subequal cycles. First cycle >1/4R, with directive septa appoximately 1/2R, second cycle <1/4R.

Radial corallites:

Tubular with dimidiate opening, they increase in size from the distal to the proximal end of the branches, more or less neatly arranged in rows or spirals. The lower wall is usually at least two times as thick as the upper wall, which may be completely reduced. Then the lower wall is developed as a lip of 1/2 to 2/3 of the corallite diameter. Between the tubular corallites lodge numerous immersed corallites. Mainly on the lower portion of the branches numerous incipient axial corallites develop into ascending branchlets. **Septa:** generally weakly developed and often reduced to a row of spines, mostly only one cycle or only the directive septa visible.

Thecae and Coenosteum:

Rows of laterally flattened spines, which often fuse to form

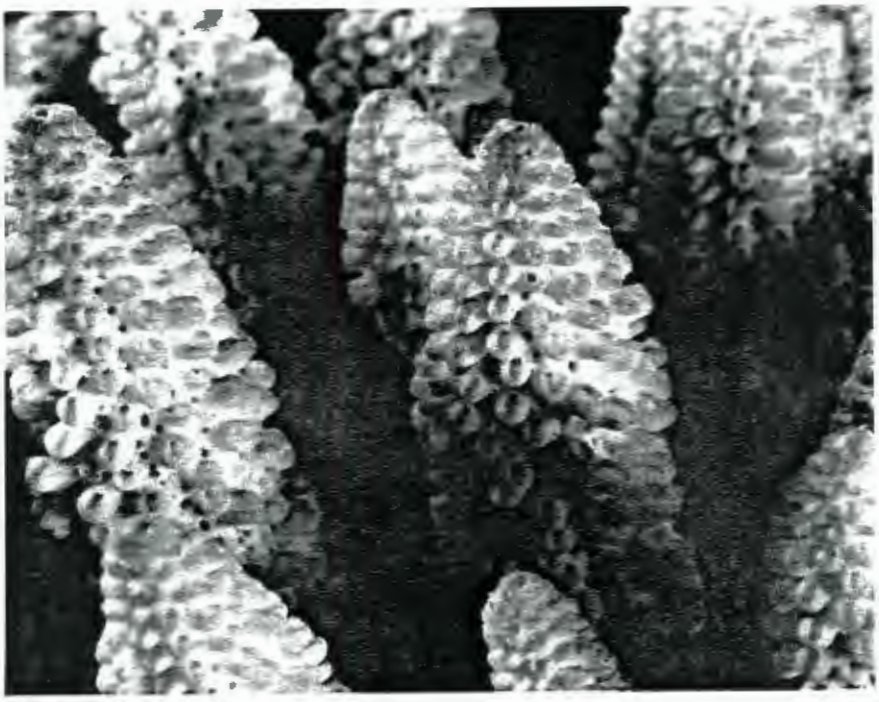


Plate 2a) Acropora (Acropora) gemmifera (Brook, 1892); ORI/AIC4(1), x1.5, from Pta. Rasa, Inhaca Island, Mozambique.

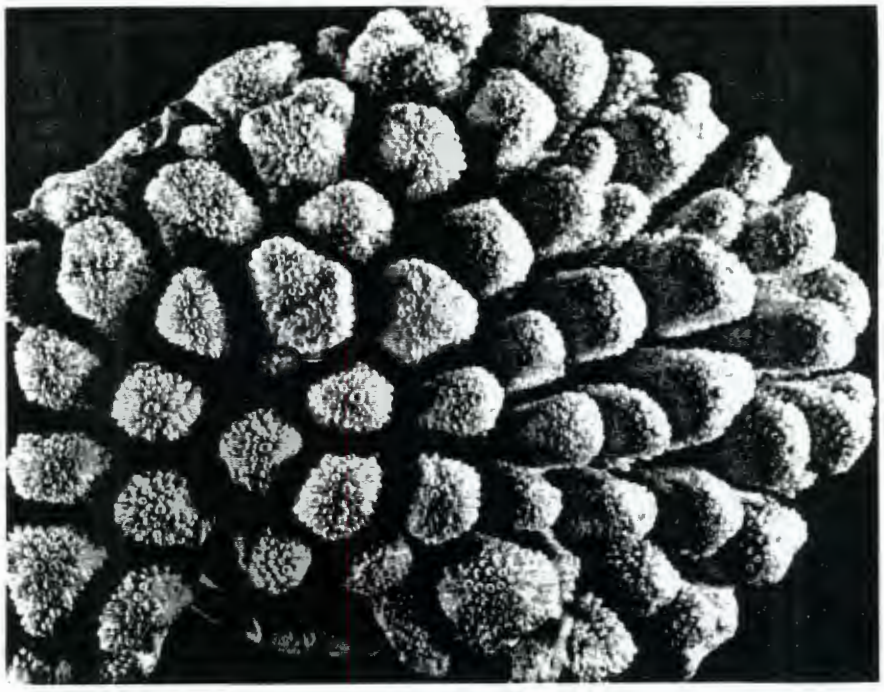


Plate 2b) Acropora (Acropora) monticulosa (Brueggemann, 1879); ORI/AIC17(1), x0.33, from Baixo 213, Inhaca Island, Mozambique.

costae, especially on the corallites.

Observations:

This widely distributed species (Red Sea to SW Pacific, Veron & Wallace, 1984) apparently has its southern distribution limit at Inhaca Island, as it has not yet been recorded in South African coral communities. Boshoff (1981) identified the present specimens as A. baeodactyla (Brook) and A. erythraea (Klunzinger).

ACROPORA (ACROPORA) MONTICULOSA (Brueggemann, 1879)

(Plate 2b)

Synonymy:

Madrepora monticulosa Brueggemann, 1879; Brook (1893).

Acropora (Acropora) monticulosa (Brueggemann); Veron & Wallace (1984); Veron (1986).

Acropora monticulosa (Brueggemann); Veron & Marsh (1988).

Material examined:

1 colony from Inhaca Island, Mozambique (ORI/AIC17(1) from Baixo 213).

Growth form:

Low corymbose with thick, stout branches. Branches are terete over most of their length and only taper at their tips.

Axial corallites:

Barely or not at all exsert (0-1.2mm), however clearly distinguishable from radial corallites. Slightly conical with outer diameter 2.1-2.7mm; calyx diameter 0.8-1.1mm. **Septa:** 2

complete cycles, first cycle >1/4R, second cycle <1/4R. Directive septa slightly larger than first cycle septa. Septa are dentate.

Radial corallites:

Appressed tubular with round to elongate opening (diameter 0.8-2.1mm). Corallites are mostly of one size and do not increase in size towards the base of the branches (as in A. gemmifera). Occasional immersed or subimmersed corallites are interspersed. The lower wall in tubular corallites is usually thickened by 1/3.

Septa: One cycle in all corallites well developed (1/4R) with at least one directive septum clearly differentiated. Where well developed, septa are dentate; in many corallites septa are reduced to a row of spines, sometimes two cycles of spines visible.

Thecae and Coenosteum:

A dense arrangement of laterally flattened spines.

Observations:

According to Wallace (pers.comm.) this species is widespread in the Central Pacific and the Indo-Australian region. It is distinct from the other members of the A. humilis group. The Axial corallites are much smaller than in all A. humilis specimens of the present series and radial corallites are very uniform in size, unlike the situation in A. gemmifera of the present collection. It is therefore unlikely that this specimen is only an extreme in growth form of either A. humilis or A. gemmifera. However, more specimens are needed for confirmation. Boshoff (1981) identified this species as A. leptocyathus (Brook).

ACROPORA (ACROPORA) DIGITIFERA (Dana, 1846)

(Plate 3a)

Synonymy:

Madrepora digitifera Dana, 1846; Brook, 1893.

Acropora digitifera (Dana); Pillai & Scheer (1976), Wallace (1978); Veron & Marsh (1988), Sheppard & Sheppard (1991).

Acropora (Acropora) digitifera (Dana); Veron & Wallace (1984); Veron (1986).

Material examined:

1 specimen from Inhaca Island Island, Mozambique (ORI/AIC14(1) from Baixo 213); 1 specimen from Bassas da India (ORI/BdI/1991-8-9).

Branching pattern:

Corymbose. From a central attachment neat, round colonies are formed with branches 7-8mm in diameter. Vertical branchlets are given off on all parts of the main branches (not only the basal parts as in A. humilis).

Axial corallites:

Exsert, conical and very conspicuous. Outer diameter 2.7-3.5mm, calyx diameter 0.7-0.9mm. **Septa:** in 2 cycles. First cycle 1/4-1/2 R, second cycle approximately 1/8 R. Second cycle is reduced in ORI/BdI/1991-8-9. The septa are dentate.

Radial corallites:

Very uniform in size all over the branches. Tubular, mostly with dimidiate opening, some long corallites with elongate opening. The lower wall is about 1/3 thicker than the upper wall. Upper wall is

often completely absent, so that the lower wall forms a slightly flaring lip of 1/2 corallite circumference. Towards the base the corallites become subimmersed to immersed. **Septa:** very reduced. Mostly only one directive septum visible and one cycle present as a low ridge, sometimes only present as a row of spines.

Thecae and Coenosteum:

Reticulate with a dense arrangement of spines.

Observations:

This species has not yet been found in South Africa, which is not surprising, as its typical habitat, shallow exposed parts of the reef (Veron, 1986), is not found in South Africa, where most coral communities grow at depths greater than 10m. Boshoff (1981) identified this species as A. indica (Brook).

The Acropora robusta group

The following species belongs to the Acropora robusta group (Veron & Wallace 1984). This group is characterized by being "...heavily calcified..., radial corallites of two sizes: the taller are tubular with round, elongate, dimidiate or nariform openings; the shorter usually have only part of the wall developed and may be regarded as sub-immersed..." They have "...very similar ranges of radial corallite structure and a virtually identical coenosteum. They are seperated on the basis of growth form differences which are usually clear in biotopes where they co-occur..." (Veron & Wallace 1984).

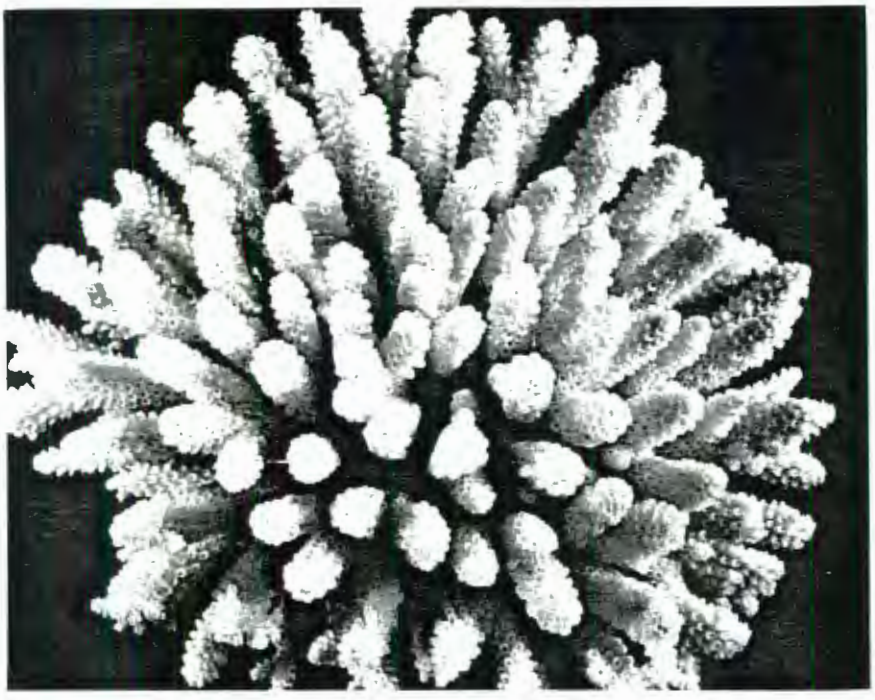


Plate 3a) Acropora (Acropora) digitifera (Dana, 1846); ORI/BdI/1991-8-9, x0.5, from Bassas da India, Lagoon.

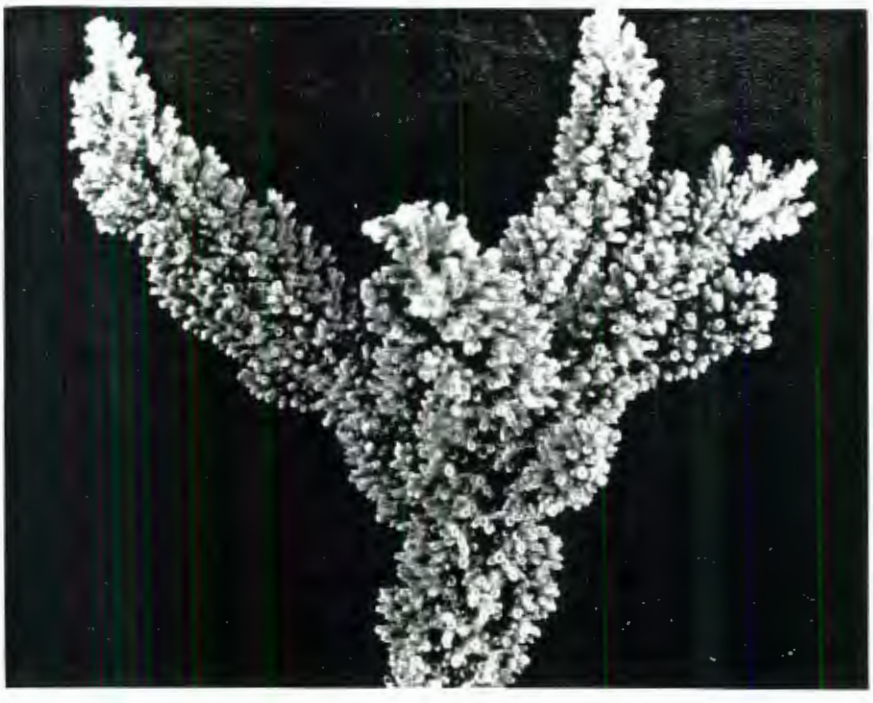


Plate 3b) Acropora (Acropora) danai (Edwards & Haime, 1860); ORI/BdI/1991-8-47, x0.33, from Bassas da India, Lagoon.

ACROPORA (ACROPORA) DANAI (Edwards & Haime, 1860)

(Plate 3b)

Synonymy:

Madrepora danai Edwards & Haime, 1860; Brook (1893).

Acropora abrotanoides (Lamarck); Pillai & Scheer (1976); Wallace (1978).

Acropora irregularis (Brook); Pillai & Scheer (1976).

Acropora danai (Edwards & Haime); Veron & Marsh (1988), Veron (1990), Sheppard & Sheppard (1991).

Acropora (Acropora) danai (Edwards & Haime); Veron & Wallace (1984), Veron (1986).

Material examined:

1 specimen from Bassas da India (ORI/BdI/1991-8-47), 9 specimens from Inhaca Island, Mozambique (ORI/AIC6(1), ORI/AIC6(3), ORI/AIC10(1), ORI/AIC15(4), ORI/AIC16(1), ORI/AIC16(2), ORI/AIC16(5), ORI/AIC16(14) from Pta.Torres, ORI/AIC5(2), ORI/AIC6(1), ORI/AIC12(1) from Baixo 213).

Branching pattern:

Thick sprawling branches, mainly horizontal, but developing short vertical branchlets, the whole colony gives a rather untidy appearance. It is difficult to describe a branching pattern from the present specimens, as most of them are only relatively small fragments. ORI/AIC12(1), a small but complete colony is used to describe a branching pattern, which is believed to be the pattern underlying the formation of the branches, which represent the other specimens. Branches are given off either horizontally or vertically, the branches soon divide and sprout numerous further

branchlets, which gives the colony a very irregular appearance. Most branchlets and branches have a tendency to grow upwards.

Axial corallites:

Thin (outer diameter 1-1.5mm), tubular, exsert up to 4mm, outer diameter 3.3-3.9mm, calyx diameter 1.1-1.4mm. **Septa:** two or only one septal cycle well developed (about 1/2 R); in the latter case the second cycle is present in form of small, reduced septa (maximum 1/8 R) or spines.

Radial corallites:

Show a wide variability from immersed to tubular. Tubular corallites usually have elongate or nariform openings and are up to 4mm exsert. Immersed or sub-immersed corallites occur all over the branches between the tubular corallites. Many of the longer first order corallites have small nariform to tubular appressed radials grouped around them and thus take the form of incipient axials. However, they do not proliferate any further. **Septa:** tubular corallites usually have one complete (up to 1/2 R) and a second, incomplete, or completely reduced, cycle. Most immersed corallites have their septa reduced to spines, which may form a complete or incomplete first cycle.

Thecae and Coenosteum:

Costate on the exsert corallites, the costae bearing spines which are large and blunt on the downward-facing side of the corallum. On the upward-facing side the costae may be completely smooth or bear only small spines. The coenosteum is spongy with large spines.

Observations:

The identification of the present specimens is not without problems. A. danai is very close to A. robusta (Dana, 1846). So close in fact, that a thorough examination of sceletal features alone need not reveal the specimen's identity, the main difference between the two mentioned species being in the secondary branching pattern (Veron & Wallace, 1984). As most specimens in the present series are small fragments, it is very difficult to get a full picture of the Branching pattern. Therefore, there is room for misidentification. The specimens in the present series show "...a major upward growth component before becoming horizontal and proliferous..." (Veron & Wallace, 1984) and are therefore considered to be A. danai. Boshoff (1981) identified the same specimens as A. brueggemanni (Brook), A. cervicornis (Lam.) and A. irregularis (Brook).

The Acropora formosa group

The following species belongs to the Acropora formosa group (Veron & Wallace 1984), which is characterized by an "...open arborescent or modified arborescent growth form..." (Veron & Wallace 1984).

ACROPORA (ACROPORA) FORMOSA (Dana,1846)

(Plate 4a)

Synonymy:

Madrepora formosa Dana, 1846.

Acropora formosa (Dana); Scheer & Pillai (1974); Pillai & Scheer (1976); Wallace (1978); Sheppard &

Sheppard (1991), Veron & Marsh (1988), Veron (1990).

Acropora (Acropora) formosa (Dana); Veron & Wallace (1984), Veron (1986).

Material examined:

5 specimens from Bassas da India (ORI/BdI/1991-8-11, ORI/BdI/1991-8-12, ORI/BdI/1991-8-13, ORI/BdI/1991-8-14, ORI/BdI/1991-8-15), 2 specimens from Inhaca Island, Mozambique (ORI/AIC15(1), ORI/AIC15(11) from Baixo 213).

Branching pattern:

Open arborescent with long, slender and straight branches. Branchlets are given off in long intervals.

Axial corallites:

Small, exsert, outer diameter 2.2-3mm, calyx diameter 0.9-1mm. **Septa:** one septal cycle usually complete (1/2R), directive septa conspicuous.

Radial corallites:

A variety of shapes from long and tubular with round opening to subimmersed and immersed. Tubular corallites tend to grow longer towards the tips of the branches (up to 6mm in length), sometimes turning into incipient axials. **Septa:** one complete cycle (size: 1/4-1/2R), ventral directive septum very conspicuous (>1/2R), septa are dentate.

Thecae and Coenosteum:

Costate on corallites, coenosteum reticulate.

Observations:

This species is very common in the lagoon of Bassas da India and

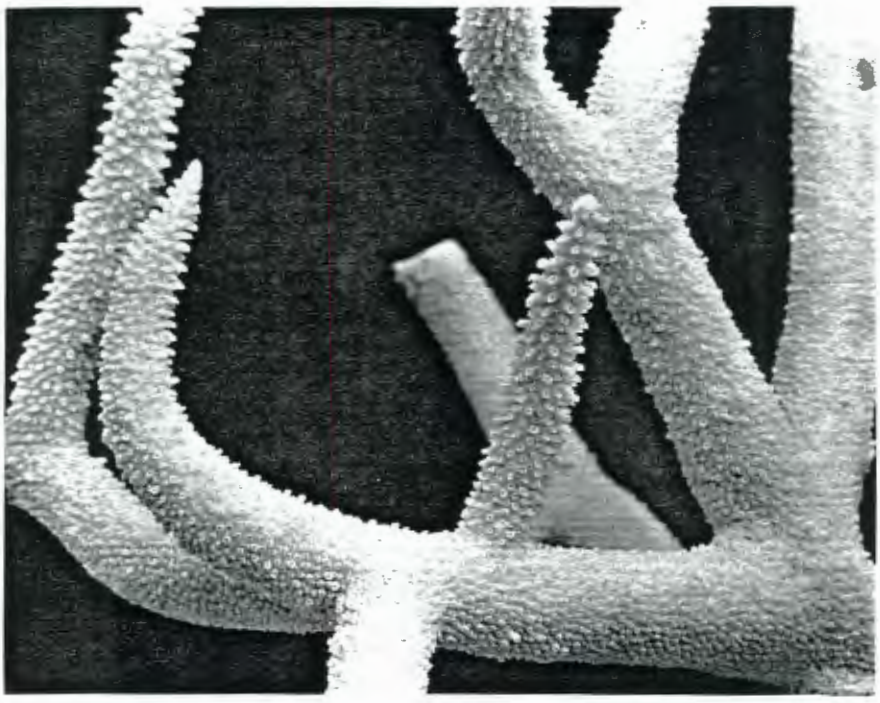


Plate 4a) Acropora (Acropora) formosa (Dana, 1846); ORI/BdI/1991-8-11, x0.5, from Bassas da India, Lagoon.

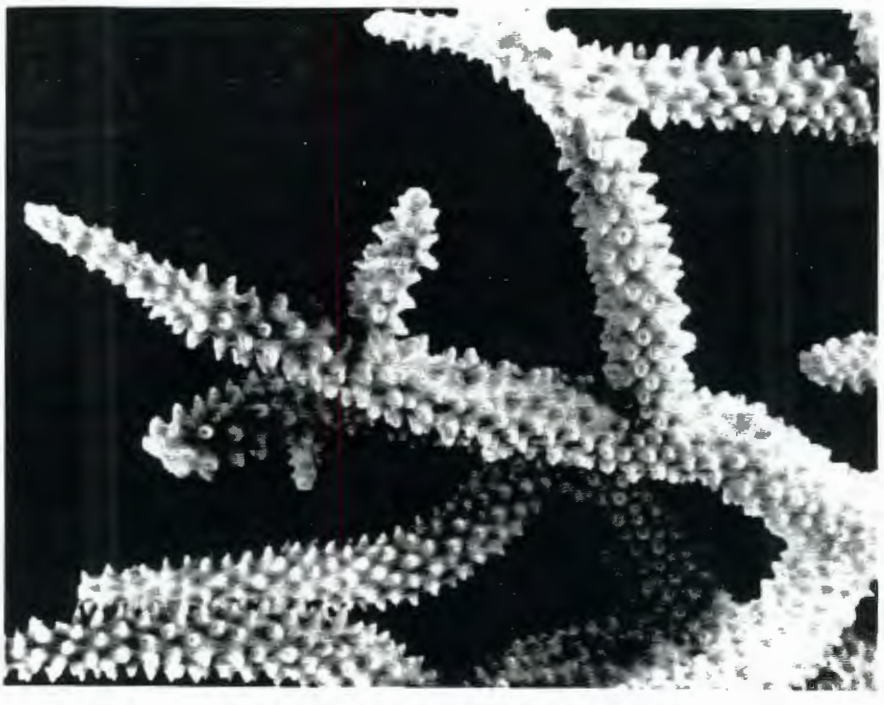


Plate 4b) Acropora (Acropora) microphthalma (Verrill, 1896); ORI/BdI/1991-8-16, x0.7, from Bassas da India, Lagoon.

present in Mozambique as far south as Inhaca Island. It is completely absent from South Africa, where suitable habitats, shallow and protected lagoonal situations, are missing. Boshoff (1981) identified the specimens from Mozambique as A. intermedia (Brook).

The Acropora horrida group

The following three species belong to the Acropora horrida group (Veron & Wallace, 1984). It is a fairly loosely knitted group with predominantly arborescent growth form, all species show some resemblance to A. horrida.

ACROPORA (ACROPORA) MICROPHTHALMA (Verrill, 1896)

(Plate 4b)

Synonymy:

Madrepora microphthalma Verrill, 1869.

Acropora microphthalma (Verrill); Wallace (1978), Veron & Marsh (1988), Veron (1990).

?Acropora teres (Verrill); Pillai & Scheer (1976).

Acropora (Acropora) microphthalma (Verrill); Veron & Wallace (1984), Veron (1986),

Material examined:

1 specimen from Bassas da India (ORI/BdI/1991-8-16), 1 specimen from Inhaca Island, Mozambique (ORI/AIC24(1) from Baixo 213).

Branching pattern:

Open arborescent with straight branches. Branches are slightly tapering. Diameter around 15mm.

Axial corallites:

Exsert, small and conical, basal diameter 2mm, distal diameter 1.3mm. **Septa:** one complete cycle (size: 1/2-1/3R), septa are dentate.

Radial corallites:

Ranging from very short, tubular appressed with elongate to nariform opening to nariform and dimidiate. The lower wall is thickened. Radials are usually shorter on the lower portion of the branches, increasing in length towards the tip (ORI/AIC24(1)). Corallites well spaced (2-4mm distance). Corallite diameter: 1.3-1.5mm, calyx diameter: 0.5-1mm. **Septa:** complete first cycle is very conspicuous (size: about 1/2R, directive septa 2/3R), strongly dentate. Second cycle usually complete (1/4R). Septa are often reduced to a row of spines.

Thecae and Coenosteum:

A dense arrangement of elaborate spines all over.

Observations:

A. microphthalma is a very conspicuous and easily recognized species due to the small, very regular and well-spaced corallites. Boshoff (1981) identified the specimen from Mozambique as A. pulchra (Brook).

ACROPORA (ACROPORA) HORRIDA (Dana, 1846)

(Plate 5a)

Synonymy:

Madrepora horrida Dana, 1846; Brook (1893).

Acropora horrida (Dana); Wallace (1978), Sheppard &

Sheppard (1991), Veron & Marsh (1988).

Acropora (Acropora) horrida (Dana); Veron & Wallace (1984), Veron (1986).

Material examined:

3 specimens from the Northern Reef Complex, RSA, 20-21m (ORI/KB/1991-9-4, ORI/KB/1991-9-5, ORI/KB/1991-9-6).

Branching pattern:

Arborescent, all three specimens are fragments of prostrate branches from sprawling colonies.

Axial corallites:

Tubular, exsert by 1.3-5.4mm; outer diameter 2.8-3.3mm, calyx diameter 1.1-1.3mm. **Septa:** well-developed first septal cycle (1/2-2/3R), in some Axials also a complete second cycle (1/4R), in others it may be incomplete or completely missing; directive septa are not very prominent.

Radial corallites:

Irregularly spaced, mostly appressed tubular with round opening; on the lower (proximal) part of the branches are numerous incipient axials; also larger radials often have small, nariform corallites at their base; the lower walls of the corallites are often thickened; **Septa:** first cycle always well developed and complete, often dentate, size 1/4-1/2R; second cycle mostly reduced.

Thecae and Coenosteum:

Distal corallites costate, costae ornamented with fine spines, coenosteum either costate or reticulate with spines; proximal corallites and coenosteum reticulate with spines.

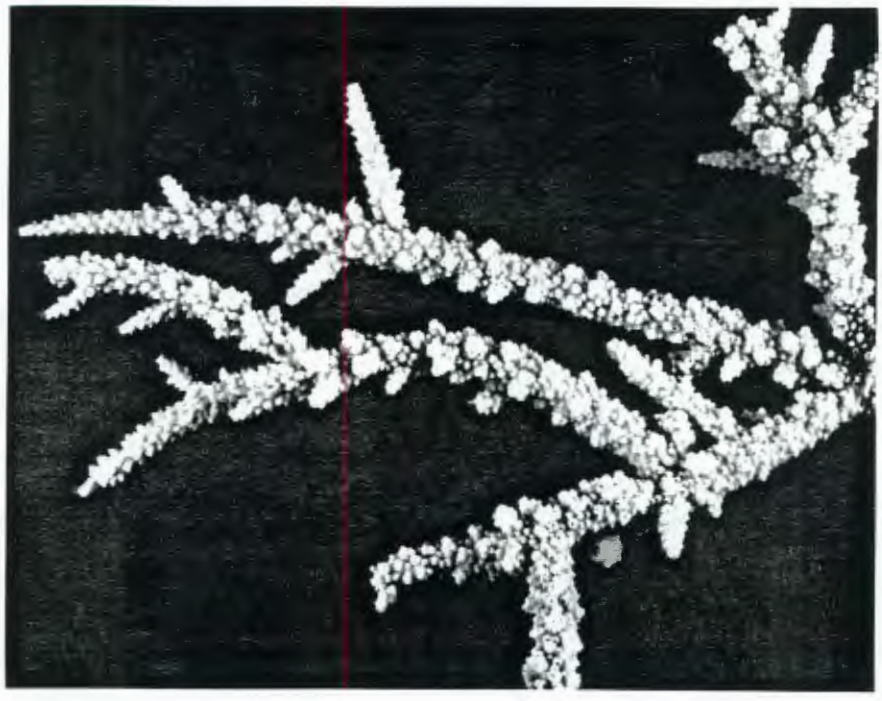


Plate 5a) Acropora (Acropora) horrida (Dana, 1846); ORI/KB/1991-9-5, x0.33, from the Northern Reef Complex (Kosi Mouth), Natal, RSA.

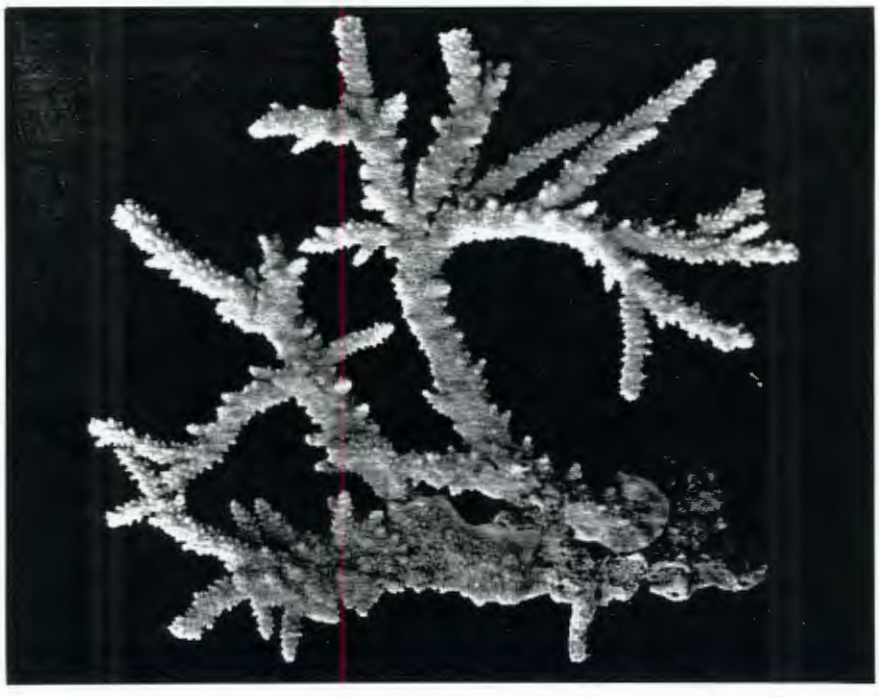


Plate 5b) Acropora (Acropora) austera (Dana, 1846); ORI/S5/1991-11-13, x0.33, from the Central Reef Complex (4-Mile Reef), Natal, RSA.

Observations:

This species has been encountered on the reefs in the Northern Reef Complex off Kosi Mouth and on 4-Mile Reef in the Central Reef Complex, where it co-occurs with A. austera in large stands. These two species look quite similar under water, A. horrida being distinguished by smaller, more appressed radials and generally longer, straighter branches.

ACROPORA (ACROPORA) AUSTERA (Dana, 1846)

(Plate 5b)

Synonymy:

Madrepora austera Dana,1846; Brook (1893).

Acropora austera (Dana); Wallace (1978), Veron & Marsh (1988).

Acropora (Acropora) austera (Dana); Veron & Wallace (1984), Veron (1986).

Material examined:

5 specimens from Inhaca Island, Mozambique (ORI/AIC5(3), ORI/AIC5(4), ORI/AIC5(5), ORI/AIC5(6), ORI/AIC15(3) from Baixo 213, ORI/AIC6(3) from Pta.Rasa). 4 specimens from the Northern Reef Complex off Kosi Mouth, RSA, 20-21m (ORI/KB/1991-9-2, ORI/KB/1991-9-3, ORI/KB/1991-9-9, ORI/KB/1991-9-15); 5 specimen from 4-Mile Reef, Central Reef Complex, RSA, 20m (ORI/S5/1991-9-35, ORI/S5/1991-11-8 through -11); 4 specimens from 2-Mile Reef, Central Reef Complex, RSA, 18m (ORI/S2/1991-7-2, ORI/S2/1991-7-3, ORI/S2/1991-7-3, ORI/S2/2-14-15/8).

Branching pattern:

Caespitose to arborescent, from a broad basal attachment branches are given off in all directions; depending on the locality, all or most branches are prostrate and sprawling (on exposed reefs, in the South African reef complexes) or branching is clearly arborescent with upward growing branches (on sheltered reefs like Baixo 213 on Inhaca Island); prostrate branches show a very clear differentiation into an upper side with numerous incipient axials and branchlets, and a downward side with immersed to sub-immersed corallites and coarse coenosteum.

Axial corallites:

Well exsert by 2-3mm and larger than radials (outer diameter around 3mm, calyx diameter around 1mm), slightly conical. **Septa:** well developed. 2 cycles (size: first cycle 1/4-1/2R, second cycle 1/8-1/4R or reduced in some axials).

Radial corallites:

Great variation in shape and size; from sub-immersed to tubular (length up to 4mm); close to the tips of the branches and on vertical branchlets most radials are tubular appressed, tending to become nariform; the lower wall is often thickened; long, tubular radials frequently become proliferous and turn into axials with nariform radials. **Septa:** well developed in tubular radials, often in two cycles (first cycle 1/4-1/2R, second cycle 1/8R or reduced); in appressed corallites septa reduced to spines with usually only one cycle developed (size around 1/4R).

Thecae and Coenosteum:

On downward facing side mostly coarse and spongy or spines all

over. On upward facing side either spines all over (ORI/AIC5(4)), or costate on corallites, reticulate with spinules in between (ORI/S2/1991-9-2).

Observations:

This species is one of the most common Acropora in South Africa, where it occurs mainly in deeper areas (from 12m down, forming large, sprawling colonies only at depths around 20m). In these areas the original branching pattern of the colonies is hardly ever discernible as the corals get frequently broken in rough seas. Most colonies take the appearance of a chaotic mass of broken and fused branches. The most typical growth form on shallow reefs (10-15m) is with only a few prostrate branches, which sprawl close to the substratum, where they are protected from wave action by other corals. Truly arborescent colonies are only occasionally found on South African reefs in deeper water (around 20m) or on Inhaca Island in Mozambique. The specimen from Bassas da India is a fragment of a caespitose colony and does not show the differentiation into upper and lower side of the branches. The colour of living specimens varies from green to yellow. Boshoff (1981) identified his specimens from Mozambique as A. brueggemanni (Brook) and A. cervicornis (Lam.).

The Acropora aspera group

Of the Acropora aspera group (Veron & Wallace, 1984), one species, A. millepora, is found in our region. The species in this group are characterized as being "...very polymorphic...having radial corallites with no upper wall and a lower wall with a rounded or

flaring lip..." (Veron & Wallace, 1984).

ACROPORA (ACROPORA) MILLEPORA (Ehrenberg, 1834)

(Plate 6a)

Synonymy:

Heteropora millepora Ehrenberg, 1834.

Acropora millepora (Ehrenberg); Wallace (1978), Veron & Marsh (1988).

Acropora (Acropora) millepora (Ehrenberg); Veron & Wallace (1984), Veron (1986).

Material examined:

1 specimen from Inhaca Island, Mozambique (ORI/AIC28(1) from Baixo 213), 3 specimens from 2-Mile Reef, Central Reef Complex, RSA, 12-15m (ORI/S2/2-3-4/6, ORI/S2/2-13-14/16, ORI/S2/2-15-16/16), 1 specimen from 9-Mile Reef, Central Reef Complex, RSA (ORI/S9/1992-1-6).

Branching pattern:

Corymbose to tabular; colonies are usually round, with equally spaced branches rising vertically in the centre, obliquely on the edge; they give a very regular, pillow shaped appearance; branches are straight and thick (diameter 9.1-14.6mm), terete or slightly tapering and rarely subdivide more than three times; a basal plate is present, which is solid and very thick.

Axial corallites:

Very conspicuous and thick-walled (outer diameter 3.5-4mm, calyx diameter 1.1-1.5mm), from barely exsert to moderately exsert (1-2.3mm). **Septa:** first cycle complete (size: 1/4-1/2R), second cycle

either complete or absent (size, when present: 1/4R).

Radial corallites:

Usually arranged in rows or spirals with only the lower wall developed as a lip, which covers 1/2 to 3/4 of the circumference, outer diameter: 1.6-3mm; on the lower parts of the branches numerous immersed corallites. **Septa:** very variable, in some coralla nearly completely reduced with only the directive septa showing; in other coralla two complete cycles (first cycle 1/2R, second cycle 1/4R) with prominent directive septa; where present septa are dentate.

Thecae and Coenosteum:

Costate on the corallites; a dense arrangement of flattened spinules on the coenosteum.

Observations:

This species is moderately common on reefs in South Africa in depths from 10 to over 20 metres.It is easily recognized by its very regular growth form with equally-spaced, thickset branches and neatly arranged radial corallites. The colour of the live animal is a deep chocolate brown. Boshoff (1981) identified his specimen from Mozambique as A. spectabilis (Brook).

The Acropora selago group

The Acropora selago group (Veron & Wallace, 1984) is represented in our area by two species: A. tenuis, which is common, A.cf.striata, which is rare. This group is characterized by "...similar radial corallites, with strongly developed lower walls

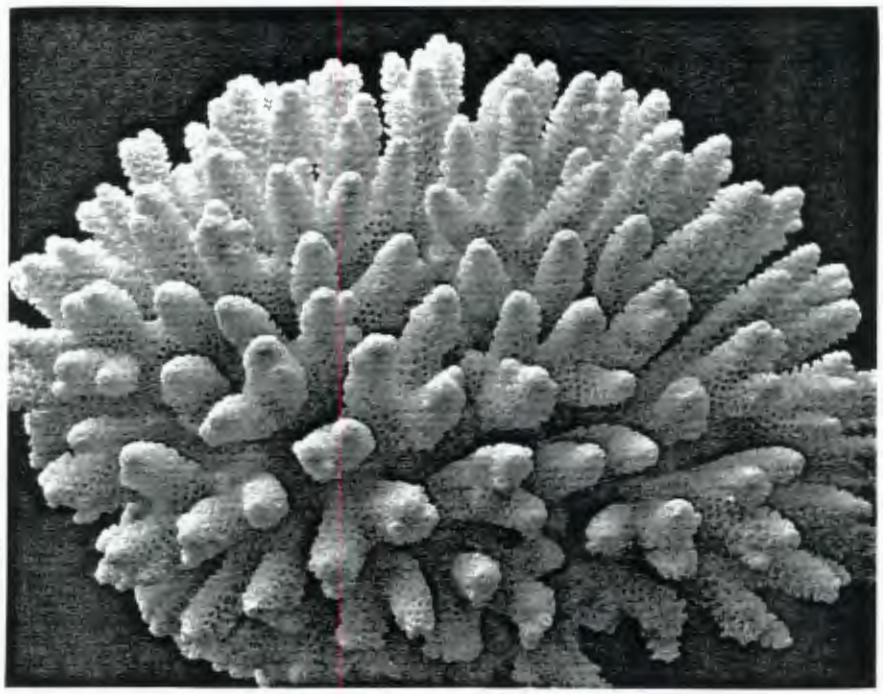


Plate 6a) Acropora (Acropora) millepora (Ehrenberg, 1834); ORI/AIC28(1) x0.33, from Baixo 213, Inhaca Island, Mozambique.

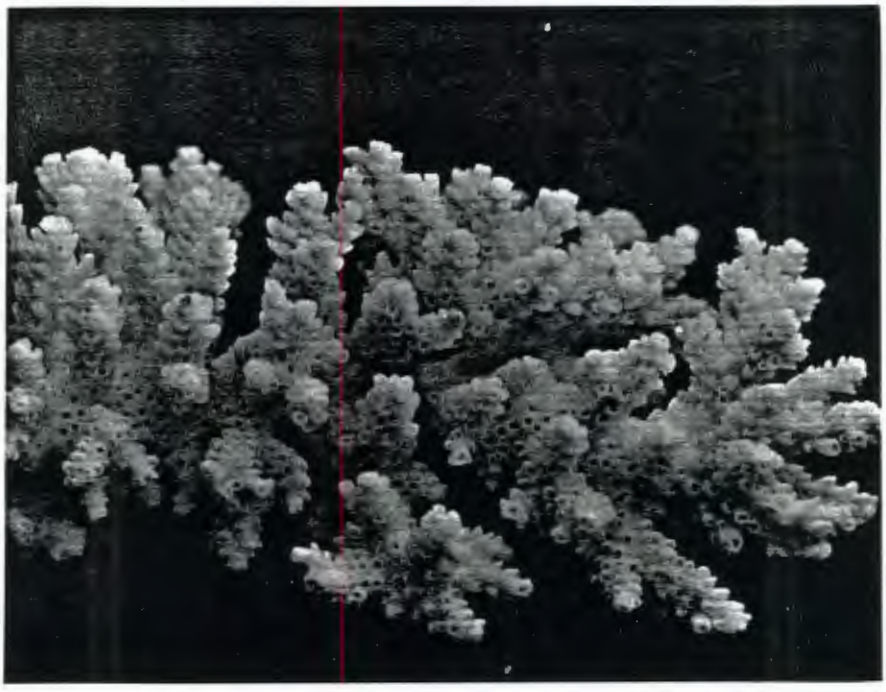


Plate 6b) Acropora (Acropora) tenuis (Dana, 1846); ORI/RS/1991-9-49, x1, from the Southern Reef Complex (Red Sands Reef), Natal, RSA.

and flaring or pointed lower lips..." (Veron & Wallace, 1984). The species can form thick, tabular colonies.

ACROPORA (ACROPORA) TENUIS (Dana, 1846)

(Plate 6b)

Synonymy:

Madrepora tenuis Dana, 1846; Brook (1893).

?Madrepora africana Brook, 1891; Veron & Wallace (1984).

Acropora tenuis (Dana); Wallace (1978), Veron & Marsh (1988).

Acropora (Acropora) tenuis (Dana); Veron & Wallace (1984), Veron (1986).

Material examined:

1 specimen from Bassas da India (ORI/BdI/1991-8-3), 2 specimens from Inhaca Island, Mozambique (ORI/AIC8(1) from Baixo 213, ORI/AIC29(2) from Pta.Torres), 1 specimen from 4-Mile Reef, Central Reef Complex, RSA (ORI/S5/1991-9-18), 3 specimens from 2-Mile Reef, Central Reef Complex, RSA (ORI/S2/1991-7-1, ORI/S2/1991-7-2, ORI/S2/2-4-5/22), 7 specimens from the Northern Reef Complex off Kosi Mouth, RSA (ORI/KB/1991-9-24, ORI/KB/1991-9-26, ORI/KB/1991-9-31 through -35).

Branching pattern:

Tabular; from a lateral attachement horizontal branches are given off first. From these originate ascending vertical branchlets, which all end in the same horizontal plane; thickness of table 25-35 mm.

Axial corallites:

Exsert by 2.4-3.4mm; outer diameter 2.4-2.9mm, calyx diameter 0.9-1mm. **Septa:** first cycle complete (1/4R), second cycle reduced, septa dentate.

Radial corallites:

Mostly tubular appressed with round, nariform or labellate opening, lower wall thickened, lip therefore slightly flaring; outer diameter 1.5-2.3mm; corallites very regularly arranged, when viewed from above they form a rosette around the axial corallite; on the horizontal part of the branches numerous immersed and sub-immersed corallites. **Septa:** first cycle complete, directive septa prominent (>1/4R), second cycle reduced in tubular corallites, well developed in sub-immersed and immersed corallites; septa dentate.

Thecae and Coenosteum:

On corallites costate, costae with a ridge of spines; coenosteum also costate, occasionally with large spines.

Observations:

This species is common on reefs between 15 and 20m in South Africa, where it forms large tables and monospecific stands of re-attached fragments. The specimens from South Africa are much more strongly calcified than the one specimen from Bassas da India, which comes from a sheltered locality in the lagoon.

The taxonomic situation of Madrepora africana Brook, 1891 is unclear as no specimens could be obtained from the Natural History Museum in London, neither for previous studies (Veron & Wallace, 1984) nor for the present one. I follow the reasoning given in

Veron & Wallace (1984) that this species is most likely a synonym of A. tenuis.

ACROPORA (ACROPORA) sp.cf.STRIATA (Verrill, 1866)

(Plate 7a)

Synonymy:

Madrepora striata Verrill, 1866

Material examined:

1 specimen from Bassas da India (ORI/BdI/1991-8-11), 1 specimen from Inhaca Island, Mozambique (ORI/AIC20(3) from Pta.Torres).

Branching pattern:

Caespito corymbose, developing into a corymbose plate; originating from a lateral attachment, a bundle of branches forms a stem, the branches then become sub-horizontal and spread out to form a table; main branches anastomose frequently; branches tapering with a diameter of 8.5 to 11.5mm, and giving off ascending, thin and tapering branchlets with a diameter of 4-6mm.

Axial corallites:

Exsert by 1.5-2mm, outer diameter 1.5-2.1mm, calyx diameter 0.7-0.9mm. **Septa:** first cycle complete (1/2-3/4R), second cycle mostly absent or incomplete.

Radial corallites:

A variety of shapes; on the lower parts of the branches sub-immersed to immersed, tubular appressed with labellate to almost dimidiate opening. Most corallites at the tips of the branchlets are tubular appressed or nariform, the lower wall is developed as a lip (1/2 circumference). **Septa:** various stages of reduction,

only first cycle, or even only one directive septum developed; septa may also be completely absent.

Thecae and Coenosteum:

Costate on distal corallites, on lower part of branches with spines, coenosteum reticulate with spines.

Observations:

This species is close to A. tenuis. It was distinguished from A. tenuis by its finer skeletal characters, thinner branches and lighter calcification. The Branching pattern is also different. A. tenuis forms larger tables with a much clearer distinction between the stem and the horizontal branches. In the present A. cf.striata specimens the main branches, which form the stem, do not fuse to the same extent as in A. tenuis, and do not become entirely horizontal but retain a strong vertical component, thus growing obliquely upwards. These branches also give off less vertical branchlets than in A. tenuis. Originally I identified these specimens as A. selago, but C. Wallace (pers.comm) suggested that due to the growth form they are more likely A. striata.

The Acropora hyacinthus group

The Acropora hyacinthus group (Veron & Wallace, 1984) is represented in our area by four species: A. cytherea, A. hyacinthus, A. paniculata and A. anthocercis. They are characterized by "...plate- or table-like colonies composed of fine, highly anastomosed, primarily horizontal branches and fine, upward projecting branchlets with small corallites..." (Veron & Wallace, 1984).

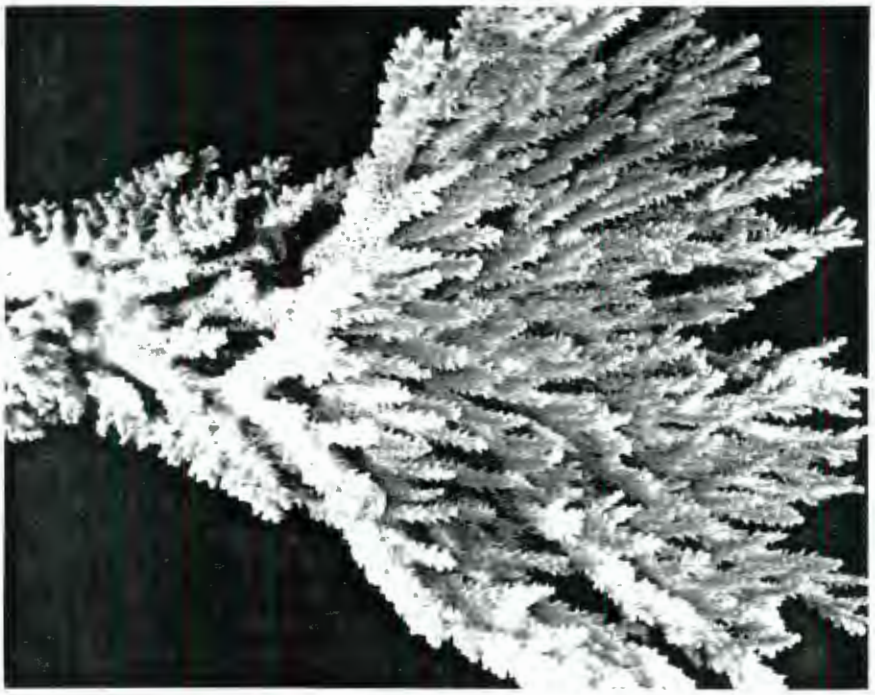


Plate 7a) Acropora (Acropora) sp. cf.striata (Studer, 1878); ORI/BdI/1991-8-11, x0.33, from Bassas da India, Lagoon.

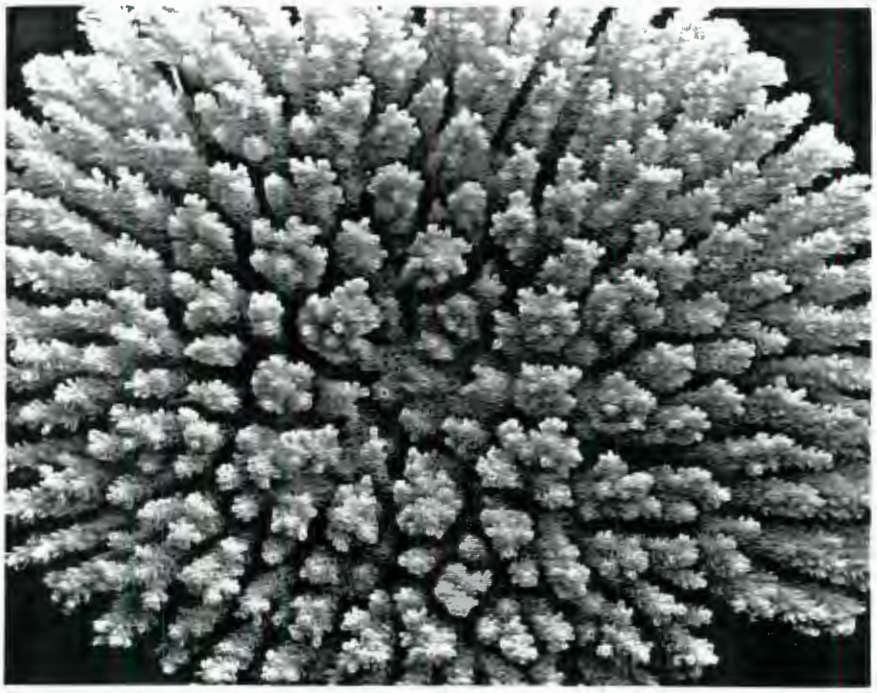


Plate 7b) Acropora (Acropora) cytherea (Dana, 1846); ORI/AIC22(1), x0.5, from Baixo 213, Inhaca Island, Mozambique.

ACROPORA (ACROPORA) CYTHEREA (Dana, 1846)

(Plate 7b)

Synonymy:

Madrepora cytherea Dana, 1846; Brook (1893).

Acropora corymbosa (Lamarck); Scheer & Pillai (1983).

?Acropora efflorescens (Dana) Pillai & Scheer (1976).

Acropora cytherea (Dana); Wallace (1978), Veron & Marsh (1988), Veron (1990), Sheppard & Sheppard (1991).

Acropora (Acropora) cytherea (Dana); Veron & Wallace (1984), Veron (1986).

Material examined:

7 specimens from Inhaca Island, Mozambique (ORI/AIC3(1), ORI/AIC22(1), ORI/AIC29(1) from Baixo 213, ORI/AIC9(1), ORI/AIC9(2) from Pta.Torres, ORI/AIC21(2) and ORI/AIC29(3) from Pta.Rasa), 1 specimen from the Northern Reef Complex off Kosi Mouth, RSA (ORI/KB/1991-9-25), 1 specimen from 9-Mile Reef, Central Reef Complex, RSA (ORI/S9/1991-7-5).

Branching pattern:

Tabular. Horizontal branches usually arise from lateral stems and anastomize frequently, and give off short, vertical branchlets (length up to 3cm, diameter 9,5 to 11.5mm); towards the periphery of the table branchlets become more scarce and point obliquely outwards.

Axial corallites:

Tubular, exsert by 1-1.9mm, outer diameter 1.5-2mm, calyx diameter around 1mm. **Septa:** one complete cycle (size: 1/2R, directive septa up to 3/4R but usually only slightly bigger than the other septa).

Radial corallites:

Tubular to tubular appressed, fairly well spaced, diameter 1.1-1.4mm, the lower wall developed as a lip (about 2/3 of circumference), in most corallites the tubular part is shorter than the lip; some corallites become long and tubular with round openings, these often develop into incipient axials; further down the branches corallites become sub-immersed to immersed. Septa: usually reduced with only one directive septum showing.

Thecae and Coenosteum:

Costate on corallites, reticulate with spinules between corallites, very porous.

Observations:

It may prove difficult to seperate A. cytherea from A. hyacinthus in small collections, especially if lightly calcified A. hyacinthus are collected. The characters used to seperate these two species in the present collection were as follows: A. cytherea is usually less heavily calcified, branches are thinner, corallites are less evenly arranged around the branchlets, the numerous long tubular corallites are missing in A. hyacinthus, and the coenosteum in A. cytherea is finer and less calcified. Boshoff (1981) identified his specimens from Mozambique as A. arcuata (Brook), A. pectinata (Brook), A. polystoma (Brook) and A. symmetrica (Brook).

ACROPORA (ACROPORA) HYACINTHUS (Dana,1846)

(Plate 8a)

Synonymy:

Madrepora hyacinthus Dana, 1846; Brook, 1892.

?Acropora pectinata (Brook); Crossland (1948).

Acropora hyacinthus (Dana); Pillai & Scheer (1976), Wallace (1978), Scheer & Pillai (1983), Veron & Marsh (1988), Veron (1990), Sheppard & Sheppard (1991).

Acropora (Acropora) hyacinthus (Dana); Veron & Wallace (1984), Veron (1986), Veron & Marsh (1988).

Material examined:

5 specimens from Inhaca Island, Mozambique (ORI/AIC2(3) and ORI/AIC21(1) from Baixo 213, ORI/AIC20(2) from Pta.Torres, ORI/AIC22(2) from Ilha dos Portugueses, ORI/AIC29(4) from Pta.Rasa), 3 specimens from the Northern Reef Complex off Kosi Mouth, RSA (ORI/KB/1991-9-27, ORI/KB/1991-9-30, ORI/KB/1991-9-36), 2 specimens from 2-Mile Reef, Central Reef Complex, RSA (ORI/S2/2-1-2/7, ORI/S2/2-1-2/15).

Branching pattern:

Similar to that described for A. cytherea, a thin plate with highly anastomosed horizontal branches, which give off short, vertical branchlets.

Axial corallites:

Tubular to slightly conical, exsert by 1.5-2.5mm, outer diameter around 2mm, calyx diameter around 1mm, **Septa:** first septal cycle

complete (1/4R), the ventral directive septum being very prominent (>1/2R), second cycle often incomplete (size: 1/8-1/4R).

Radial corallites:

From tubular with round opening to appressed tubular with labellate opening. The lip is around 2/3 of the corallite circumference and slightly flaring; on the base of the axial corallite, numerous small, nariform radials form a "rosette" (Wallace, 1978); towards the base of the branchlets numerous sub-immersed to immersed corallites. **Septa:** usually well developed, in larger corallites two cycles (size: 1/4R, directive septa: 1/2R), in small, nariform corallites often only one septal cycle discernible; in sub-immersed and immersed corallites septa well developed.

Thecae and Coenosteum:

Costate on axial and radial corallites, reticulate with spines between corallites.

Observations:

This species can be easily confused with A. cytherea (see above). The present specimens from South Africa represent the ecotype "from exposed biotopes" (Veron & Wallace, 1984). AIC20(2) from Inhaca Island represents the ecotype "from turbid habitats" (Veron & Wallace, 1984). Boshoff (1981) identified his specimens from Mozambique as A. anthocercis (Brook), A. patula (Brook) and A. polystoma (Brook).

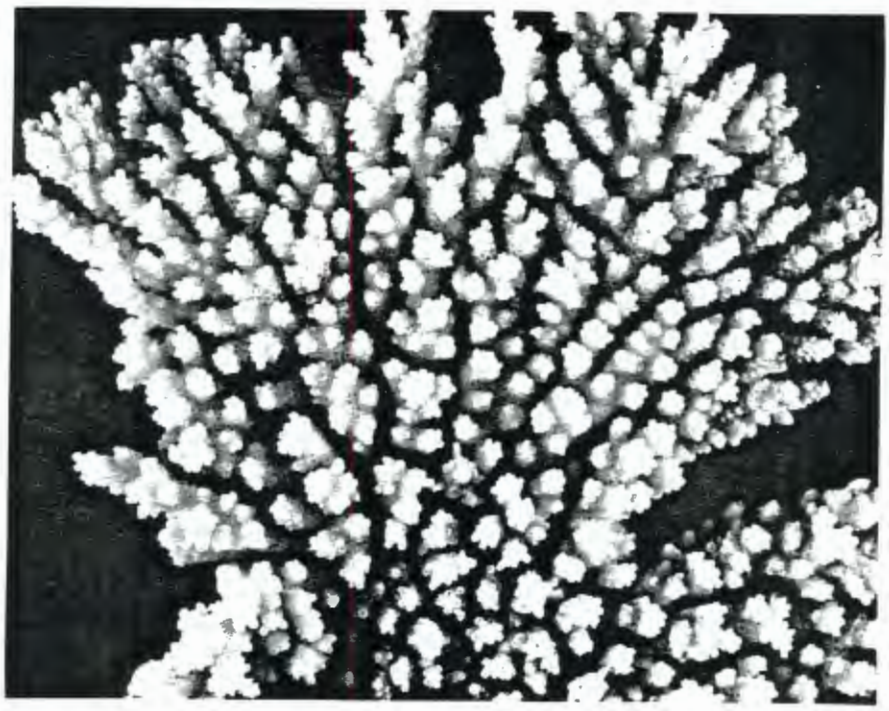


Plate 8a) Acropora (Acropora) hyacinthus (Dana, 1846); ORI/KB/1991-9-30, x0.33, from the Northern Reef Complex off Kosi Mouth, Natal, RSA.

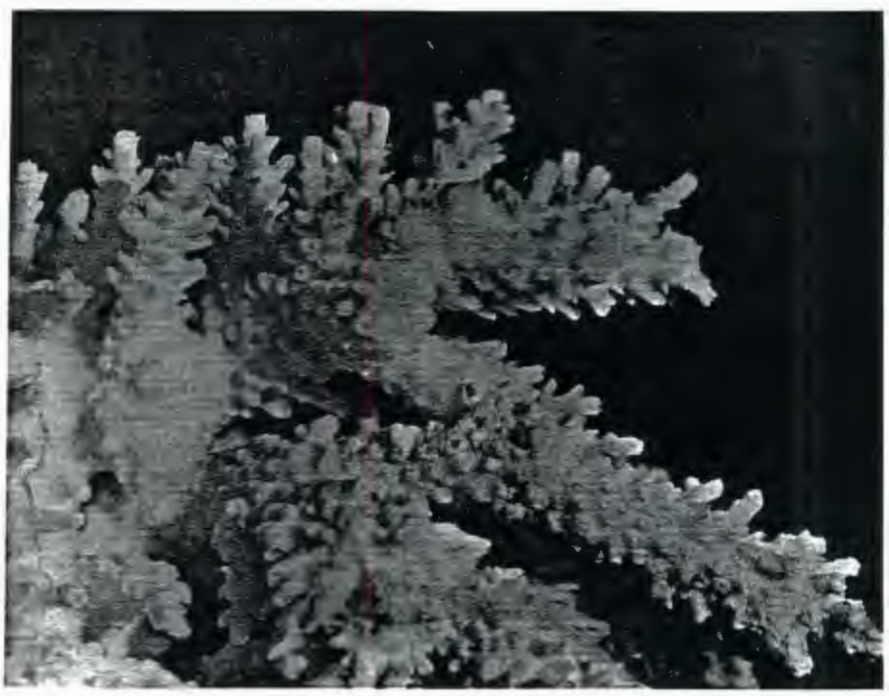


Plate 8b) Acropora (Acropora) paniculata Verrill, 1902; ORI/BdI/1991-8-27, x1.3, from Bassas da India, Lagoon.

ACROPORA (ACROPORA) PANICULATA Verrill, 1902

(Plate 8b)

Synonymy:

Acropora paniculata Verrill, 1902; Veron & Marsh (1988), Veron (1990).

Acropora (Acropora) paniculata Verrill; Veron & Wallace (1984), Veron (1986).

Material examined:

1 specimen from Bassas da India (ORI/BdI/1991-8-27).

Branching pattern:

The specimen is a young colony, corymbose and on its way to forming a table; a lateral attachment is giving off branches which show a clear tendency to spread in a table-like manner.

Axial corallites:

Tubular, exsert by 1.9-4mm, outer diameter 1.8-1.9mm, calyx diameter 0.7-0.9mm. **Septa:** first cycle very well developed (size: 2/3-1R, sometimes fusing in the centre), second cycle abortive.

Radial corallites:

A variety of shapes and sizes; mostly tubular and long with round, elongate or nariform opening, corallites increase in size towards the tip where they are very long and conspicuous, interspersed between tubular corallites numerous subimmersed and immersed corallites, especially on the lower part of the branches; long corallites often become proliferous and form incipient axials. **Septa:** highly variable, from completely reduced to two complete cycles present (size: 2/3-1R), which may fuse in the centre; directive septa usually very distinct.

Thecae and Coenosteum:

Costate on corallites; open reticulate with a spongy appearance between corallites.

Observations:

This species has not been recorded on the african mainland coast. It is easily distinguished from the other members of the A. hyacinthus group by the numerous long, and very irregular radial corallites. It is the only species in this group showing this feature.

ACROPORA (ACROPORA) ANTHOCERCIS (Brook, 1893)

(Plate 9a)

Synonymy:

Madrepora anthocercis Brook, 1893.

Acropora anthocercis (Brook); non Boshoff (1981), Veron & Marsh (1988).

Acropora (Acropora) anthocercis (Brook); Veron & Wallace (1984), Veron (1986), Veron & Marsh (1988).

Material examined:

2 specimens from the Northern Reef Complex off Kosi Mouth (ORI/KB/1991-9-20, ORI/KB/1991-9-52).

Branching pattern:

Corymbose plates with lateral attachment, the horizontal branches show a tendency to anastomize. Horizontal branches very thick relative to the vertical branchlets (horizontal branches: 15-25mm diameter, vertical branchlets: 7-10mm diameter); vertical branchlets evenly spaced, about 10mm from each other, straight and

short (12-28mm), some giving off secondary branchlets, thinner at their bases due to numerous protuberant radials at the top (5-8mm at the bases, 6-10mm at the tips).

Axial corallites:

Well exsert (2.5-3.2mm), tubular, diameter 2.2-2.8mm, calyx diameter 0.6-0.9mm; **Septa:** always well developed, usually in two cycles (first cycle: 1/2R, directives: 2/3R, second cycle: 1/4R), second cycle may be reduced to a row of spines; in specimens with particularly well developed septa (ORI/KB/1991-9-52) a columella is formed where the septa meet.

Radial corallites:

A variety of shapes and sizes; on the horizontal branches mostly sub-immersed to immersed, with occasional tubular corallites interspersed; on the vertical branchlets increasing in length towards the tips; corallites at the branchlet bases are mostly appressed tubular with round opening and short (1-3mm), in the upper third they become long and tubular (4-6mm) and turn into incipient axials; frequently two radials at the opposite sides of a branchlet become incipient axials, which then gives the branchlet a flattened appearance; corallites at the very top the branchlets are nariform. **Septa:** equally well developed as in the axials, always two cycles with prominent directives (first cycle 1/2R, directives 2/3R, second cycle 1/4R).

Thecae and Coenosteum:

Corallite walls covered with rows of fine spinules which may fuse to form costae, coenosteum also covered with fine spinules.

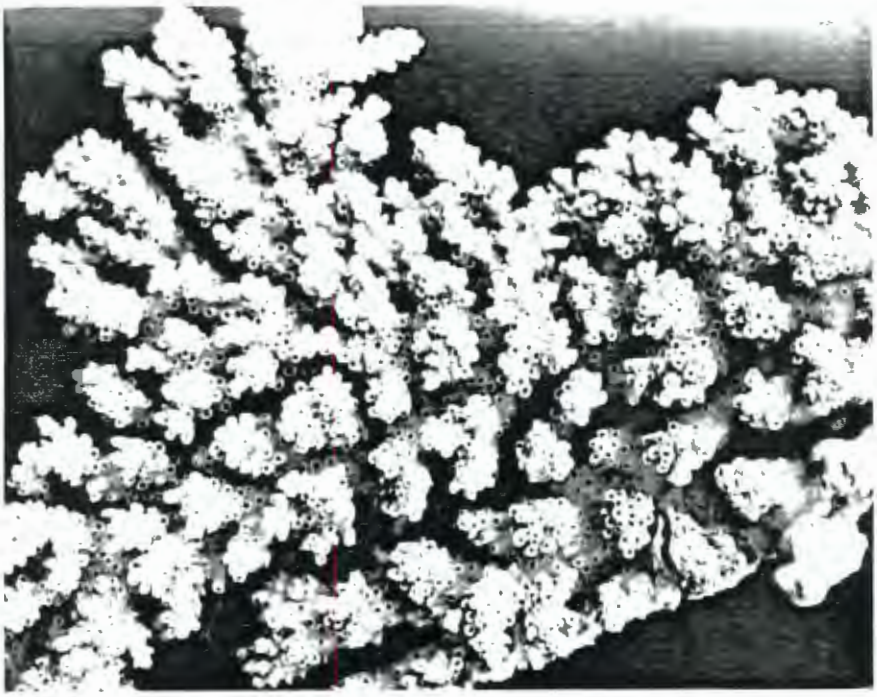


Plate 9a) Acropora (Acropora) anthocercis (Brook, 1893), ORI/KB/1991-9-20, x0.9, from the Northern Reef Complex off Kosi Mouth, Natal, RSA.

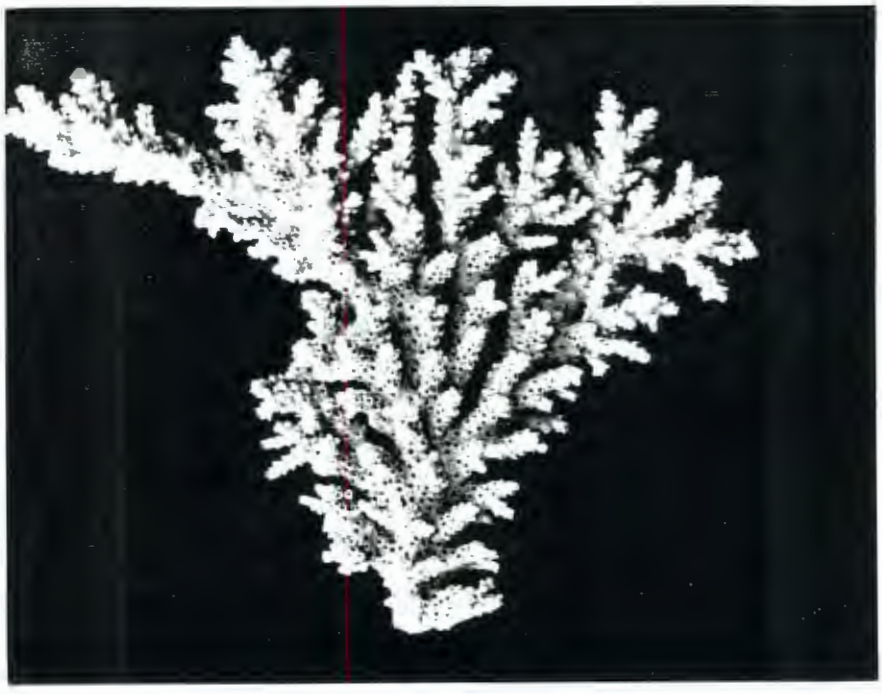


Plate 9b) Acropora (Acropora) latistella (Brook, 1892); SAM-H4639, x0.5, from 4-Mile Reef, Central Reef Complex, Natal, RSA.

Observations:

The present specimens fit very well the original description given in Brook (1893). This species is close to A. hyacinthus but can be separated by the different structure and arrangement of its radial corallites and a different coenosteum. A. anthocercis is more heavily calcified and resembles a bigger version of A. hyacinthus. On Reefs it occurs in deep Acropora assemblages together with A. austera, A. tenuis, A. hyacinthus and A. clathrata.

The Acropora latistella group

The Acropora latistella group (Veron & Wallace, 1984) is represented in our area by three species. This is a very loosely defined group having in common "...small appressed corallites and slender branches..." (Veron & Wallace, 1984). The growth form may vary from corymbose to tabular.

ACROPORA (ACROPORA) LATISTELLA (Brook, 1892)

(Plate 9b)

Synonymy:

Madrepora latistella Brook, 1892; Brook (1893), Gardiner (1898).

Acropora latistella (Brook); Hoffmeister (1925), Wallace (1978), Veron & Marsh (1988), Veron (1990).

Acropora (Acropora) latistella (Brook); Veron & Wallace (1984).

Material examined:

2 specimens from 4-Mile Reef, Central Reef Complex, Natal, RSA

(SAM-H-4639, SAM-H-4641).

Branching pattern:

Corymbose to tabular; all South African specimens are fragments from tables with lateral attachment; the vertical branchlets are well spaced, slender and terete; they end in the same horizontal plain.

Axial corallite:

Tubular, well exsert by about 2 mm, corallite diameter 0.8-1.1mm, calyx diameter 0.7-1mm. **Septa:** One cycle well developed 1/-3/4R; second cycle may be incomplete; septa are dentate.

Radial corallites:

Tubular appresssed with round to dimidiate opening; neatly arranged along the vertical branchlets, usually in rows or spirals; towards the bases of the branchlets they tend to become immersed. **Septa:** One complete cycle (up to 1/2R), an incomplete second cycle usually present (size up to 1/4R).

Thecae and Coenosteum:

Costate to broken costate on the corallites; spinules on the coenosteum.

Observations:

This species is common on the deeper reefs in South Africa, where it co-occurs with the other tabular species, sometimes in dense stands. It can be seperated from the Acropora hyacinthus group by the larger size of the corallites and the terete branches. A. latistella is also easily seperated from A. nana by its tabular growth form and the shorter branches.

ACROPORA (ACROPORA) NANA (Studer, 1878)

(Plate 10a)

Synonymy:

Madrepora nana Studer, 1878.

Acropora (Acropora) nana (Studer). Veron & Wallace (1984); Veron (1986).

Material examined:

2 specimens from Bassas da India (ORI/BdI/1991-8-4, ORI/BdI/1991-8-5), 2 specimens from Inhaca Island, Mozambique (ORI/AIC20(1), ORI/AIC30(1)).

Branching pattern:

Corymbose, branches originating directly from an encrusting base, branch diameter 12-14mm, slightly tapering towards the tip. The central branches are very straight, branches on the periphery only slightly oblique in the beginning, then tending to grow vertically upwards, this uniform vertical growth giving the colonies a hemispherical, very neat appearance.

Axial corallites:

Exsert; tapering, lower diameter 2.1mm, distal diameter 1.9mm, calyx diameter 0.9-1.1mm. **Septa:** 2 septal cycles, size of the first cycle 1/8-1/4R, directive septa 1/4R, second cycle often only as a row of spines.

Radial corallites:

Appressed tubular with round to elongate openings, becoming nariform towards the tips of the branches; arranged in lines, and subimmersed on the lower parts of the branches; in ORI/AIC20(3) most radials are labellate, on the lower part of the branches

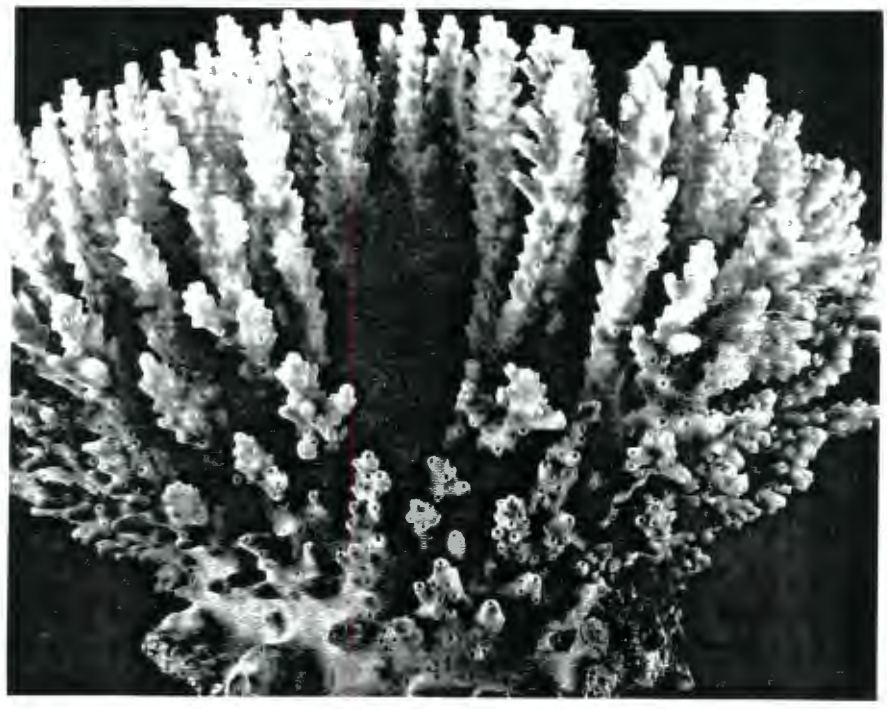


Plate 10a) Acropora (Acropora) nana (Studer, 1878); ORI/BdI/1991-8-48, x0.7, from Bassas da India, lagoon.

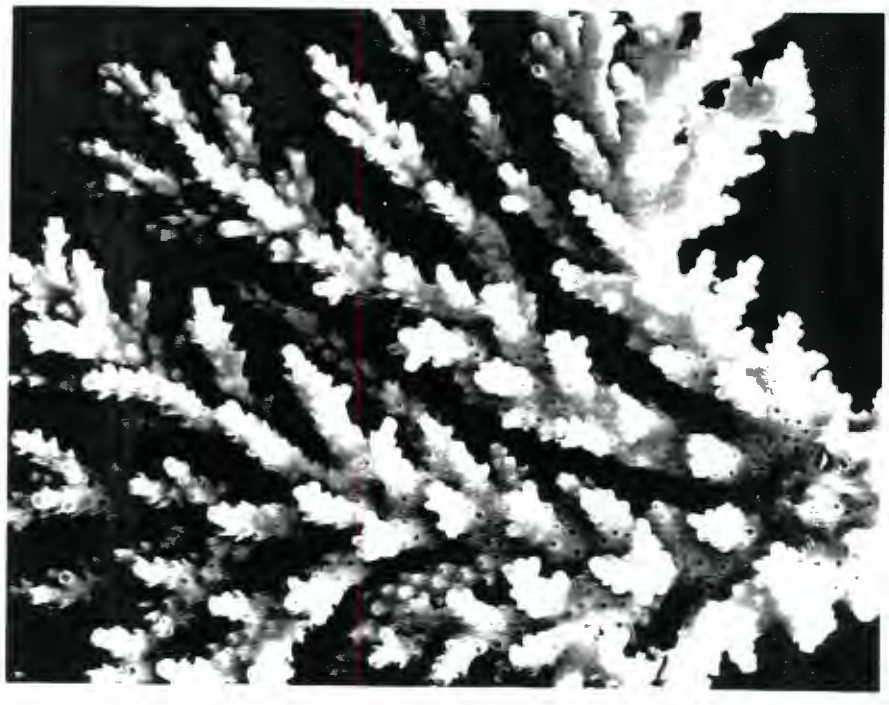


Plate 10b) Acropora (Acropora) aculeus (Dana, 1846); ORI/KB/1991-8-19, x0.7, from the Northern Reef complex off Kosi Mouth, Natal, RSA.

(especially the peripheral ones) very long (up to 10mm) tubular corallites often developed, becoming proliferous. Septa: one cycle (size:1/8-1/4R) with distinct directive septa or completely reduced.

Thecae and Coenosteum:

Reticulate with spines all over, the basal part of the spines frequently fuse.

Observations:

This species is apparently absent from South Africa, where conditions may be too rough, as A. nana is a species of protected waters (Veron & Wallace, 1984). A.nana was previously only recorded in the Indian Ocean at Cocos-Keeling Islands and around Australia. Boshoff identified his specimen from Mozambique as A. tizardi (Brook).

ACROPORA (ACROPORA) sp. cf.ACULEUS (Dana, 1846)

(Plate 10b)

Synonymy:

Madrepora aculeus Dana, 1846; Brook (1893).

Acropora aculeus (Dana); Wallace (1978).

Acropora (Acropora) aculeus (Dana). Veron & Wallace (1984), Veron (1986), Veron & Marsh (1988).

Material examined:

2 specimens from the Northern Reef Complex off Kosi Mouth, RSA, 20m (ORI/KB/1991-8-19, ORI/KB/1991-9-28).

Branching pattern:

Tabular, arising from a lateral attachment which gives off

horizontal branches that anastomize irregularly; short, vertical branches grow at intervals of about 1cm; thickness of table about 2cm.

Axial corallites:

Exsert by 2 to 4mm, slightly conical, outer diameter 2.5mm, calyx diameter 1.1mm. On horizontal part of branchlets long ascending Axials with very few Radials are often found, also near the growing edge there is often a strong development of incipient Axials. **Septa:** Septa present as a row of spines, or, when developed, size is 1/8-1/4R, directive septa usually longer (size 1/4-1/2R), second cycle septa reduced to spines.

Radial corallites:

On the horizontal part of the branches mostly sub-immersed to immersed, on branchlets mostly appressed tubular with round or nariform opening, towards the tips of the branchlets often nariform, lower wall sometimes developed as a lip. **Septa:** present, although often only in form of spines; two cycles may be present, the second however often reduced; directive septa mostly clearly distinguishable.

Thecae and Coenosteum:

Costate on the corallites, costae sometimes with spines; coenosteum broken costate or, on horizontal branches, reticulate with spines.

Observations:

This species is apparently uncommon as it was only found in the Northern Reef Complex off Kosi Mouth, RSA, on the deep parts of the reef in a diverse Acropora assemblage. More specimens are

needed to confirm the presence of this species without doubt.

The Acropora nasuta group

The Acropora nasuta group (Veron & Wallace, 1984) is represented in South East Africa by three species. This group is well defined by "...similar corallite and coenosteal structures ... corymbose or caespito-corymbose growth form, which can develop into side attached plates or stalked tables..." (Veron & Wallace, 1984).

ACROPORA (ACROPORA) NASUTA (Dana, 1846)

(Plate 11a)

Synonymy:

Madrepora nasuta Dana, 1846; Brook (1893).

Acropora nasuta (Dana); Wallace (1978), Sheer & Pillai (1983), Veron & Marsh (1988), Sheppard & Sheppard (1991).

Acropora (Acropora) nasuta (Dana); Veron & Wallace (1984), Veron (1986).

Material examined:

1 specimen from Bassas da India (ORI/BdI/1991-8-10), 1 specimen from Inhaca Island, Mozambique (ORI/AIC8(6) from Baixo 213), 3 specimens from the Northern Reef Complex off Kosi Mouth, RSA, 10m (ORI/KB/1991-9-7, ORI/KB/1991-9-8, ORI/KB/1991-9-16).

Branching pattern:

Corymbose in all specimens, thick, tapering branches, diameter 10-16mm.

Axial corallites:

Tubular, exsert by 1.8-2.4mm, tapering, outer diameter 2.9-3.9mm, calyx diameter 1-1.5mm. **Septa:** 2 complete septal cycles (first cycle 1/4R, second cycle 1/8R), ventral directive septum very prominent (1/2R).

Radial corallites:

Appressed tubular with round, elongate to nariform openings; corallites arranged in rows with decreasing size towards the branch tips; the lower walls are slightly better developed than the upper walls; on the main branches subimmersed corallites occur, however not in such number and regularity as in A. secale. **Septa:** reduced, first cycle usually present, though often only as a row of spines, the ventral directive septa are very prominent.

Thecae and Coenosteum:

Reticulate with spines, the basal parts of the spines may fuse to form costae.

Observations:

This species is uncommon in South Africa, where it has only been recorded in the Northern Reef Complex off Kosi Mouth, and Mozambique. It seems to be more common on Bassas da India. It is not easily distinguished from A.valida, the more regular radials being the best distinguishing tool. Boshoff (1981) identified his specimens from Mozambique as A. concinna (Brook).

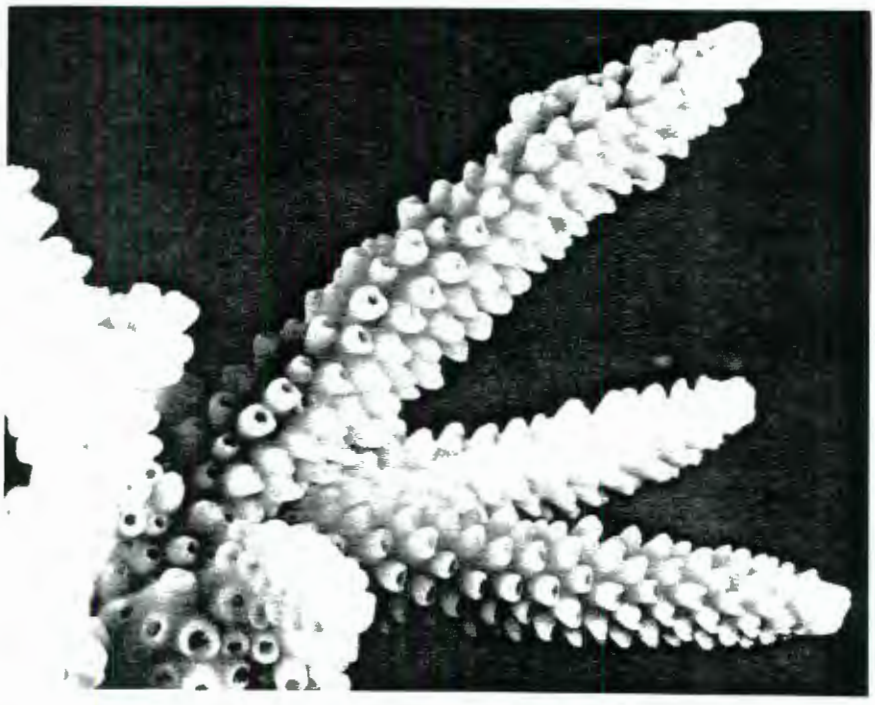


Plate 11a) Acropora (Acropora) nasuta (Dana, 1846); ORI/KB/1991-9-16, x1.3, from the Northern Reef Complex off Kosi Mouth, Natal, RSA.

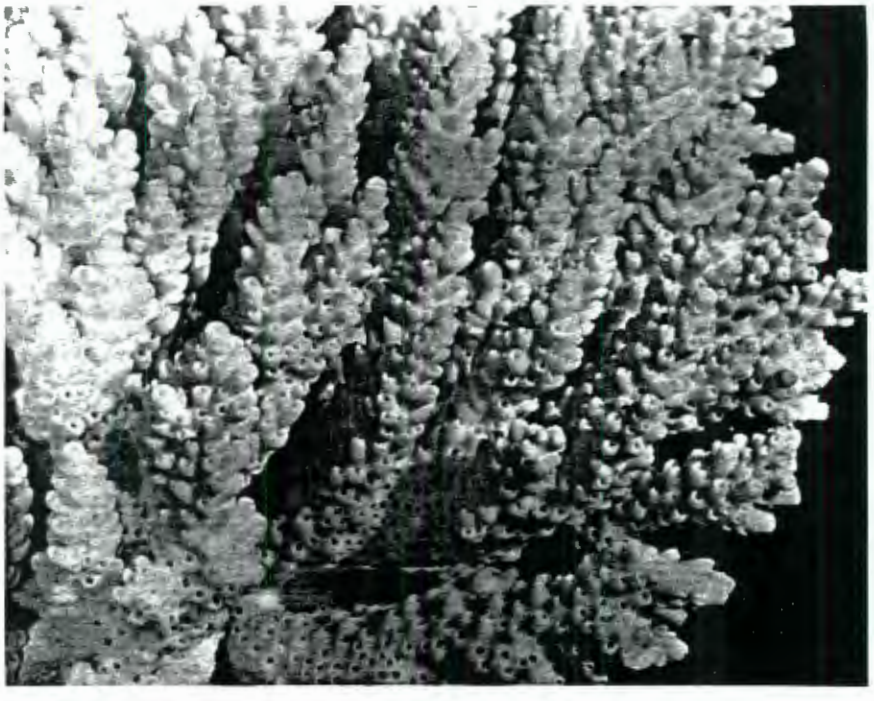


Plate 11b) Acropora (Acropora) valida (Dana, 1846); ORI/AIC8(3), x1, from Ilha dos Portugueses, Mozambique.

ACROPORA (ACROPORA) VALIDA (Dana, 1846)

(Plate 11b)

Synonymy:

Madrepora valida Dana, 1846; Brook (1893).

Madrepora variabilis Klunzinger, 1879; Brook (1893).

Acropora variabilis (Klunzinger); Scheer & Pillai (1974), Pillai & Scheer (1976); Scheer & Pillai (1983), Wallace (1978).

Acropora (Acropora) valida (Dana); Veron & Wallace (1984), Veron (1986).

Acropora valida (Dana); Veron & Marsh (1988), Veron (1990), Sheppard & Sheppard (1991).

Material examined:

1 specimen from Inhaca Island, Mozambique (ORI/AIC8(3) from Ilha dos Portugueses).

Branching pattern:

Corymbose, corallum very compact and pillow-like, branches thick with diameter from 11.3 to 13.1mm, tapering, very regularly arranged.

Axial corallites:

Exsert by 2.1-3mm, conical, slightly tapering (basal diameter 2.6-3.3mm, apical diameter 2.2-2.9mm). **Septa:** 2 complete cycles, first cycle 1/2R, second cycle 1/4R, directive septa 3/4R.

Radial corallites:

Mostly appressed tubular with nariform opening although some tubular with round opening; interspersed are numerous sub-immersed to immersed corallites with nariform opening; corallites are

usually not arranged in rows (as in A. nasuta). Septa: vary greatly between corallites; two complete cycles (size:1/4R) in tubular corallites, in nariform corallites either only directive septa showing or completely reduced. Two septal cycles present as rows of spines in immersed corallites.

Thecae and Coenosteum:

Densely arranged, elaborate spines all over; the spines are arranged in neat rows on the corallites.

Observations:

The present specimen was identified as A.valida mainly because of the differences in the arrangement and structure of radial corallites from the specimens in the present A.nasuta series. In A. valida Radials are not arranged in rows and are more appressed. Also nariform openings occur more regularly on ORI/AIC8(3) as do sub-immersed and immersed corallites. On the present specimen these sub-immersed or immersed corallites are found on all regions of the branches, while in the A. nasuta series they are mainly confined to the proximal parts. The thecae and coenosteum of AIC8(3) are however very similar to those in the A. nasuta series. According to Veron & Wallace (1984) in A. valida "corallites are costate, with fine or coarse costae without prominent synapticulae". This situation however is not reflected in the photographs of their specimens (Fig.859 and 862), where rows of spicules on the thecae are shown. I did not find any differences in thecal and coenosteal structure between A. nasuta and A.valida. The difference between the two species seem to be entirely in the

arrangement and shape of radial corallites. Boshoff (1981) identified his specimen from Mozambique as A. concinna (Brook).

ACROPORA (ACROPORA) SECALE (Studer, 1878)

(Plate 12a)

Synonymy:

Madrepora secale Studer, 1871.

Acropora secale (Studer). Scheer & Pillai (1974).

Acropora (Acropora) secale (Studer). Veron & Wallace (1984); Veron (1986).

Material examined:

2 specimens from Bassas da India (ORI/BdI/1991-8-6, ORI/BdI/1991-8-9), 3 specimens from Inhaca Island Mozambique (ORI/AIC8(2), ORI/AIC8(4) from Pta.Rasa, ORI/AIC13(4) from Baixo 213).

Branching pattern:

Judging from the present fragments, the Branching pattern is corymbose to caespito-corymbose, the branches thick and tapering; diameter of main branches 22.9mm, that of secondary branches 14.9-16.5mm.

Axial corallites:

Thick walled, outer diameter 3.6-4.4mm, calyx diameter 1-1.9mm, exsert to 3mm, slightly conical. **Septa:** 2 complete septal cycles (size of first cycle: 1/4 to 1/2R, size of second cycle 1/4R), directive septa very distinct.

Radial corallites:

Long tubular corallites with round opening (up to 5mm exsert) alternate with very short (up to 1mm) or subimmersed tubular

radials. The long radials reach their maximum size at about half the branch length, decreasing again in size towards the tips and the bases; long and tubular radials often have very small nariform corallites attached; the long, tubular radials are often arranged in rows, the sub-immersed corallites are irregularly arranged. **Septa:** 2 septal cycles, first cycle complete (size: up to 1/4R), second cycle often reduced and septa only visible as a row of spines.

Thecae and Coenosteum:

Reticulate with spines all over, spines have elaborate tips.

Observations:

This species seems to have its southern limits at Inhaca Island, as it has not yet been recorded in South Africa. It is easily distinguished from the other two species in this group by its long, robust and tubular radial corallites. In A. nasuta and A. valida the radial corallites are always appressed tubular. Boshoff (1981) identified his specimens from Mozambique as A. concinna (Brook), A. diversa (Brook) and A. gravida Dana.

The Acropora divaricata group

The Acropora divaricata group (Veron & Wallace, 1984) is represented by two species. The group is held together by "...similar nariform to tubo-nariform radial corallites and a similar coenosteum between corallites which is reticulate....on corallites the coenosteum is costate or broken costate....or else consists of dense spinules..." (Veron & Wallace, 1984).

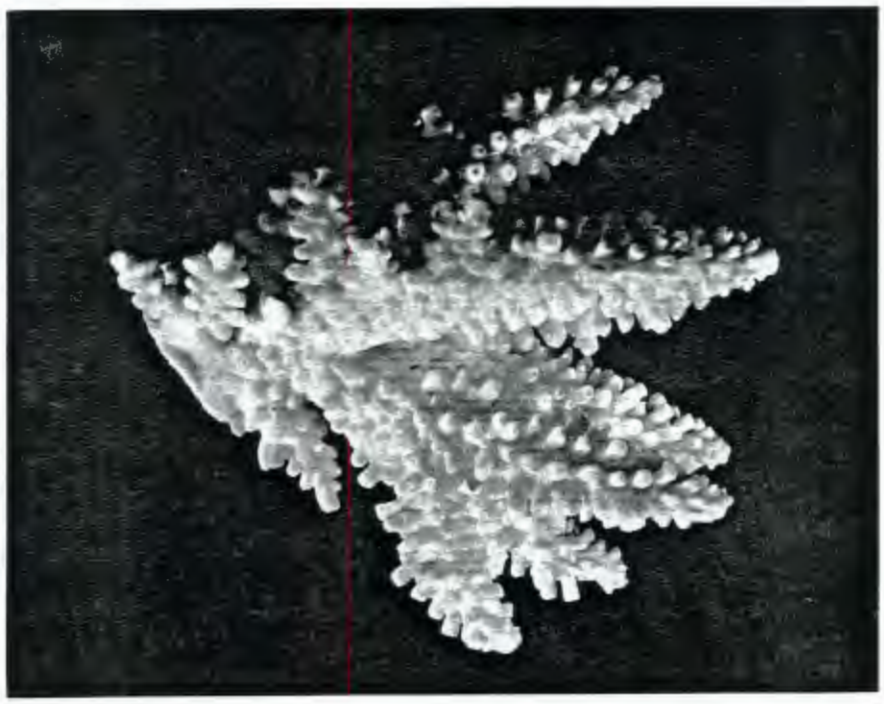


Plate 12a) Acropora (Acropora) secale (Studer, 1878); ORI/BdI/1991-8-9, x0.7, from Bassas da India, lagoon.

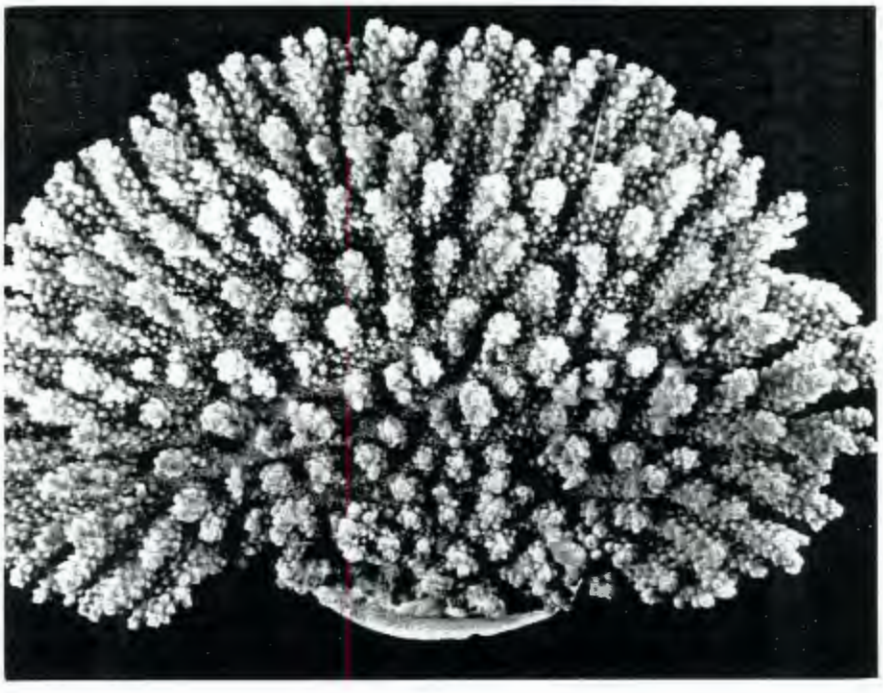


Plate 12b) Acropora (Acropora) clathrata (Brook, 1891); ORI/AIC26(1), x0.5, from Pta. Zavora, Mozambique.

ACROPORA (ACROPORA) CLATHRATA (Brook, 1891)

(Plate 12b)

Synonymy:

Madrepora clathrata Brook, 1891; Brook (1893).

Madrepora orbicularis Brook, 1892; Brook (1893).

Madrepora vasiformis Brook, 1893.

Acropora vasiformis (Brook); Pillai & Scheer (1976), Boshoff (1981).

Acropora clathrata (Brook); Wallace (1978), Veron & Marsh (1988), Sheppard & Sheppard (1991).

Acropora (Acropora) clathrata (Brook); Veron & Wallace (1984); Veron (1986).

Material examined:

3 specimens from Inhaca Island, Mozambique (ORI/AIC19(2) and ORI/AIC26(1) from Baixo 213, ORI/AIC31(2) from Pta.Torres), 1 specimen from Pta.Zavora (ORI/AIC26(1)), Mozambique coast, 4 specimens from 9-Mile Reef, Central Reef Complex, RSA (ORI/S9/1991-9-48, ORI/S9/1991-9-39, ORI/S9/1992-1-6, ORI/S9/1992-1-7), 1 specimen from Northern Reef Complex, RSA (ORI/KB/1991-9-42).

Branching pattern:

Vasiform to horizontal plates in one or more tiers; horizontal branches are completely fused, leaving only small pores, if any, between them; vertical branchlets either completely absent or reduced to an axial with only one or two rosettes of Radials (rarely longer than 5mm); the fusion of horizontal branches is

visible even in very young colonies (ORI/S9/1991-9-48, ORI/KB/1991-9-42).

Axial corallites:

Moderately to markedly exsert (1-3.5mm), conical, tapering from 2.5-3mm at the base to 1.9-2.1mm at the top, calyx diameter 0.6-1mm, **Septa:** 1 cycle, which is not always complete (about 1/4R), septa dentate.

Radial corallites:

From tubular through appressed tubular with round, elongate or dimidiate opening on branches and branchlets (where visible); on the plate and along the lines of fusion of branches, mostly subimmersed to immersed; corallites are very unequal, especially on the plates, where no branchlets are formed, long tubular corallites then alternate with sub-immersed and immersed ones; corallites are very crowded on the upper sides of the plates (spacing 1-3mm), on the lower sides they vary from few and far between (spacing 5-10mm) to relatively dense (spacing up to 5mm); their walls have a rounded margin. **Septa:** generally more reduced in tubular corallites where only one cycle is present, on sub-immersed and immersed corallites mostly one cycle but often two cycles are present with prominent directives, septa dentate (1/8-1/2R).

Thecae and Coenosteum:

Rows of laterally flattened spines on the corallites, reticulate inbetween.

Observations:

All present specimens correspond very closely to the description

and illustration of A. vasiformis in Brook (1893). This species is very common on all reef types and always forms solid plates, irrespectively of exposure and turbidity. It is very uniform across the whole region (although no specimens were available from Bassas da India) and cannot be confused with any other species. Boshoff (1981) identified his specimens from Mozambique as A. ocellata (Klunz.), A. recumbens (Brook) and A. vasiformis (Brook).

The Acropora florida group

Of the two species in this group, one is present in South Africa. The typical feature for this group is the secondary Branching pattern, with numerous short secondary branchlets.

ACROPORA (ACROPORA) FLORIDA (Dana, 1846)

(Plate 13a)

Synonymy:

Madrepora florida Dana, 1846.

Madrepora gravida Dana, 1846; Brook, 1893.

Acropora florida (Dana); Wallace (1978).

Acropora (Acropora) florida (Dana); Veron & Wallace (1984), Veron & Marsh (1988).

Material examined:

3 colonies from Two-Mile Reef, Central Reef Complex, Natal, RSA (SAM-H-4638, SAM-H-4640, SAM-H-4642).

Branching pattern

Main branches corymbose to arborescent, normally covered with short secondary branchlets, in some instances clearly approaching

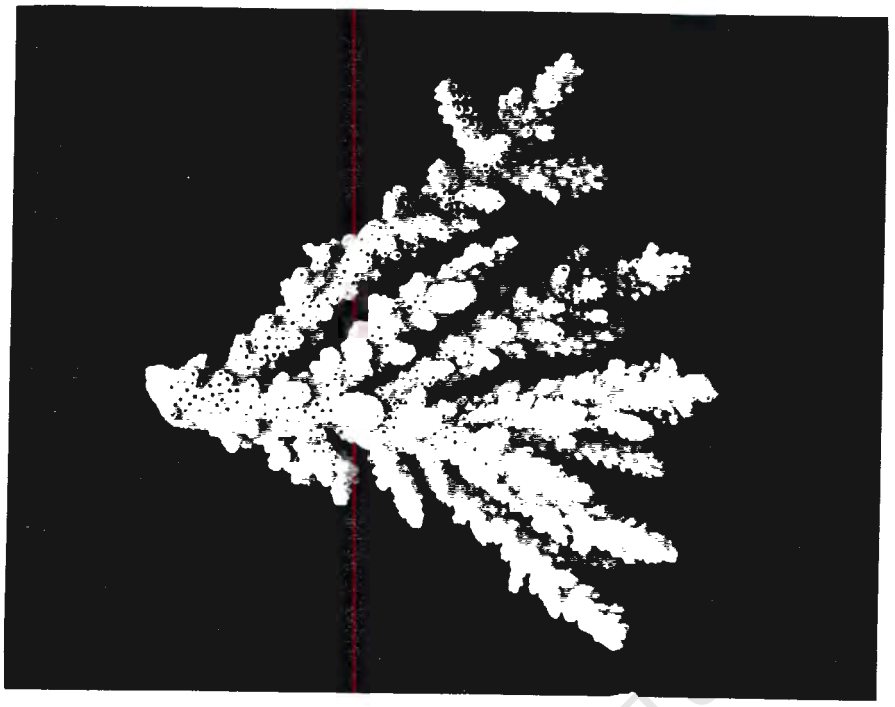


Plate 13a) Acropora (Acropora) florida (Dana, 1846); SAM-H-4638, X0.5, from 2-Mile Reef, Central Reef Complex, Natal, RSA.

a hispidose condition. Secondary branchlets are better developed on the upper surface of the branches and may be completely suppressed on the lower surface.

Axial corallite:

Diameter 2-3mm, calyx diameter 1-1.5mm, moderately exsert (exsert up to 3mm). **Septa:** usually two well developed cycles; first cycle up to 2/3R, second cycle 1/4-1/2R.

Radial corallites:

Ranging from tubular through tubular appressed to almost nariform at the branch tips; especially on the secondary branchlets the Radials are very uniform. **Septa:** in most corallites two well-developed cycles present; size of first cycle up tp 1/2R, second cycle up to 1/4R.

Thecae and Coenosteum:

On corallites costate or broken costate; between the corallites generally reticulate.

Observations:

This species is moderately common on South African reefs. It co-occurs with A. austera, from which it can be told by the numerous secondary branchlets and the generally smaller growth form of A. florida. In some instances, on the deeper reefs, it may prove tricke to seperate A. austera with numerous incipient axials from A. florida with short secondary branches, which in this environment also grow arborescent. In shallow areas of the reefs A. florida seems to be more common than A. austera.

Discussion

The Acropora fauna of South-East Africa consists mainly of species with wide distribution in the Indo-Pacific. The fauna of Southern Mozambique (23 species) was found to be richer than the South African fauna (14 species). This can probably be explained by the more complex reef-structure in Mozambique, which offers more ecological niches and therefore provides habitat for a greater number of species. Coral communities in South Africa are subjected to very uniform environmental conditions, due to the type of substratum they grow on. These fossil sand dunes (Ramsey & Mason, 1990) principally only allow differentiation into shallow and deep coral communities. Most species of Acropora are only common in deep communities, as wave action in shallow water appears to be too strong (see Part II and Part III, Chapter 1). The Acropora fauna of the investigated areas also allows conclusions to be

drawn about their ecological structuring. This is particularly well illustrated in South Africa, where most species of the Acropora humilis-group, which are typical for shallow reef-crest environments are missing, as well as typical lagoonal calm water species, as A. formosa and A. microphthalma.

The Acropora fauna of southern Mozambique and Bassas da India is very similar, with that on Bassas da India being only marginally richer. Sofar only one species exclusive to Bassas da India was found. It appears that the Acropora fauna of the southern Indian Ocean is very homogenous, as most species, which were found in South East Africa occur all accross the Indian Ocean as far as Western Australia (Sheppard, 1987; Veron & Marsh, 1988). If the Australian-Indonesian region is considered as the centre of diversity, most coral species must have reached Africa by a process of island-hopping, driven by the major oceanic currents (Jokiel & Martinelli, 1992). The similarity of the Bassas da India and Mozambiquan coral faunas could be regarded as indicator that a similar process might have linked the faunas of Madagascar and South East Africa via Bassas da India. The peripheral situation of the South East African Acropora-fauna could theoretically also lead to the development of pripheral endemism (Rosen, 1988). This will be proven in the next chapter, with the description of four new species from the area.

The numerous new distribution records of species, which were previously not known to occur so far west and south, prove that we still have a lot to learn about the biogeography of this important genus.

DESCRIPTION OF FOUR NEW SPECIES IN THE HARD CORAL GENUS ACROPORA Oken, 1815 (Scleractinia: Astrocoeniina: Acroporidae) FROM SOUTH-EAST AFRICA

Abstract

Four new species in the scleractinian coral genus Acropora, A.natalensis, A.mossambica, A.sordiensis and A.branchi are described from South-East Africa. Two species occur both in South Africa and Mozambique (A.natalensis and A.mossambica), two species are only known from northern Natal in South Africa (A.sordiensis and A.branchi). A. branchi and A.mossambica are intertidal species and were collected from permanent tidal pools. A.sordiensis and A.natalensis are strictly subtidal species.

Introduction

The hard-coral genus Acropora is the biggest extant coral genus with a world-wide distribution within the coral reef belt. It is very common and ecologically one of the most important coral genera in most reef-coral communities. The African hard-coral fauna generally and the Acropora fauna in particular are poorly known as little detailed research has been conducted in the area. Brook (1893) has described one species from South Africa, A. africana, which was later synonymized with A.tenuis by Veron & Wallace (1984). The exact type locality of Brook's species is unknown, as he states "South Africa, Cape of Good Hope". No hermatypic coral species occur however in the cold waters of the Cape Province. It is possible that the specimen actually came from Natal (where A.tenuis occurs) or from somewhere else and the labels got mixed up. Boshoff (1981) has given a list of species occurring in Mozambique, but much of his paper needs taxonomic revision.

In South East Africa the genus Acropora is at its southern limits of distribution in the Indo-Pacific faunal province and often has to exist in marginal conditions; no true coral reefs are developed here. Two of the new species described here were collected in tidal pools, far away from the next important coral assemblages. It seems plausible that the extreme environment encountered within South-East African reef systems has had an influence on speciation.

Methods

Most specimens were collected in South Africa by the author. The type specimens of A.mossambica were collected by P.Boshoff in

Mozambique and housed at the Oceanographic Research Institute in Durban.

Morphometric descriptions and terms follow the terminology used by Wallace (1978) and Veron & Wallace (1984).

The collections in which the specimens are housed, are indicated by a prefix to the inventory number: SAM is South African Museum in Cape Town, ORI is Oceanographic Research Institute in Durban.

ACROPORA (ACROPORA) NATALENSIS sp.nov.

HOLOTYPE: SAM-H-4629 from 21m depth on Four Mile Reef, Central Reef Complex, Natal, RSA (27°30'S, 33°35'E); fragment of a two tiered, tabular colony (the fragment is from the upper tier), maximum length 370mm, maximum width 205mm, maximum height 105mm.

PARATYPES: SAM-H-4630 from 22m depth on Four-Mile Reef, Central Reef Complex, Natal, RSA (27°30'S, 33°35'E); fragment of a single tiered, tabular colony, maximum length 200mm, maximum width 90mm, maximum height 41mm.

ORI/KB/1991-9-37 from 22m at Kosi Bay, Northern Reef Complex, Natal, RSA (26°55'S, 33°45'E); fragment of a tabular colony.

SAM-H-4631 from 20m at Four-Mile Reef, Central Reef Complex, RSA (27°30'S, 33°35'E), fragment of a tabular colony.

ORI/S5/1991-11-12 from 21m at Four-Mile Reef, Central Reef Complex, RSA (27°30'S, 33°35'E), fragment of a tabular colony.

ORI/A1C7(2) from Pta.Torres, Inhaca Island, Mozambique (26°10'S, 32°30'E), fragment of a tabular colony; collector P.Boshoff.

ORI/A1C3(7) from Xai Xai, Mozambique (25°8'S, 33°42'E), fragment of a tabular colony; collector P.Boshoff.

DESCRIPTION

Branching Pattern:

All specimens show a tendency to form horizontal plates, usually only one-tiered but in large colonies also two-tiered (SAM-H4629), with frequent anastomoses and partial fusion of horizontal branches, which are flattened and spreading; the degree of fusion shows a progression from ORI/A1C7(3) - ORI/A1C7(2) - SAM-H-4631 - ORI/S5/1991-11-12 - ORI/KB/1991-9-37. Vertical branches are round, 7.2-11.3mm in diameter, 11.3-35.6mm long and give off spreading secondary branchlets which also fuse in ORI/KB/1991-9-37; the development of horizontal branches is very regular in the Holotype and gets increasingly irregular through the Paratype series, for example SAM-H-4630 has only about half the vertical branches fully developed, while the others are short to rudimentary; this gives the colony a very uneven appearance.

Axial corallites:

Conical, slightly tapering, markedly exsert by 2.5-4mm; diameter 2-2.5mm; calyx diameter 0.6-0.8mm; in the Holotype numerous axials missing, possibly due to Parrotfish predation. **Septation:** in two cycles, septa dentate, size 1/2-1/3 calyx radius, directive septa are prominent (1/2-2/3 calyx radius); in the Holotype and ORI/KB/1991-9-37 only one dentate septal cycle with prominent directive septa is present in most axials.

Plate 1:

A) Acropora (Acropora) natalensis, SAM-H-4629, Holotype, from 4-Mile Reef, South Africa, x0.3.

B) Acropora (Acropora) natalensis, SAM-H-4630, from 4-Mile Reef, Central Reef Complex, South Africa, x0.75.

C) Acropora (Acropora) natalensis, ORI/KB/1991-9-37, from the Northern Reef Complex off Kosi Mouth, South Africa, x0.75.

D) Acropora (Acropora) natalensis, ORI/AIC7(2), from Pta. Torres, Inhaca Island, Mozambique, x1.5.

Plate 1 a, b, c & d

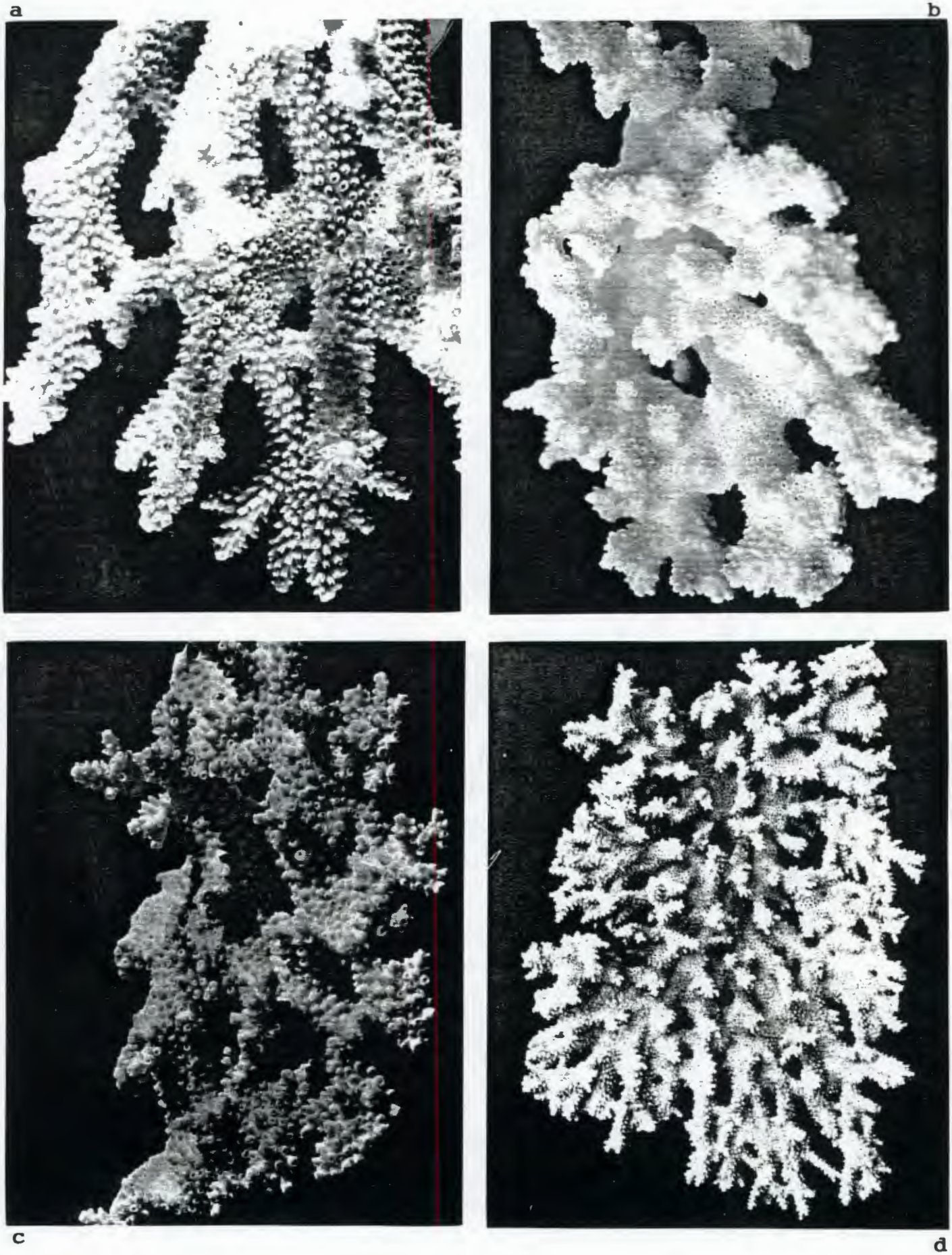


Plate 2:

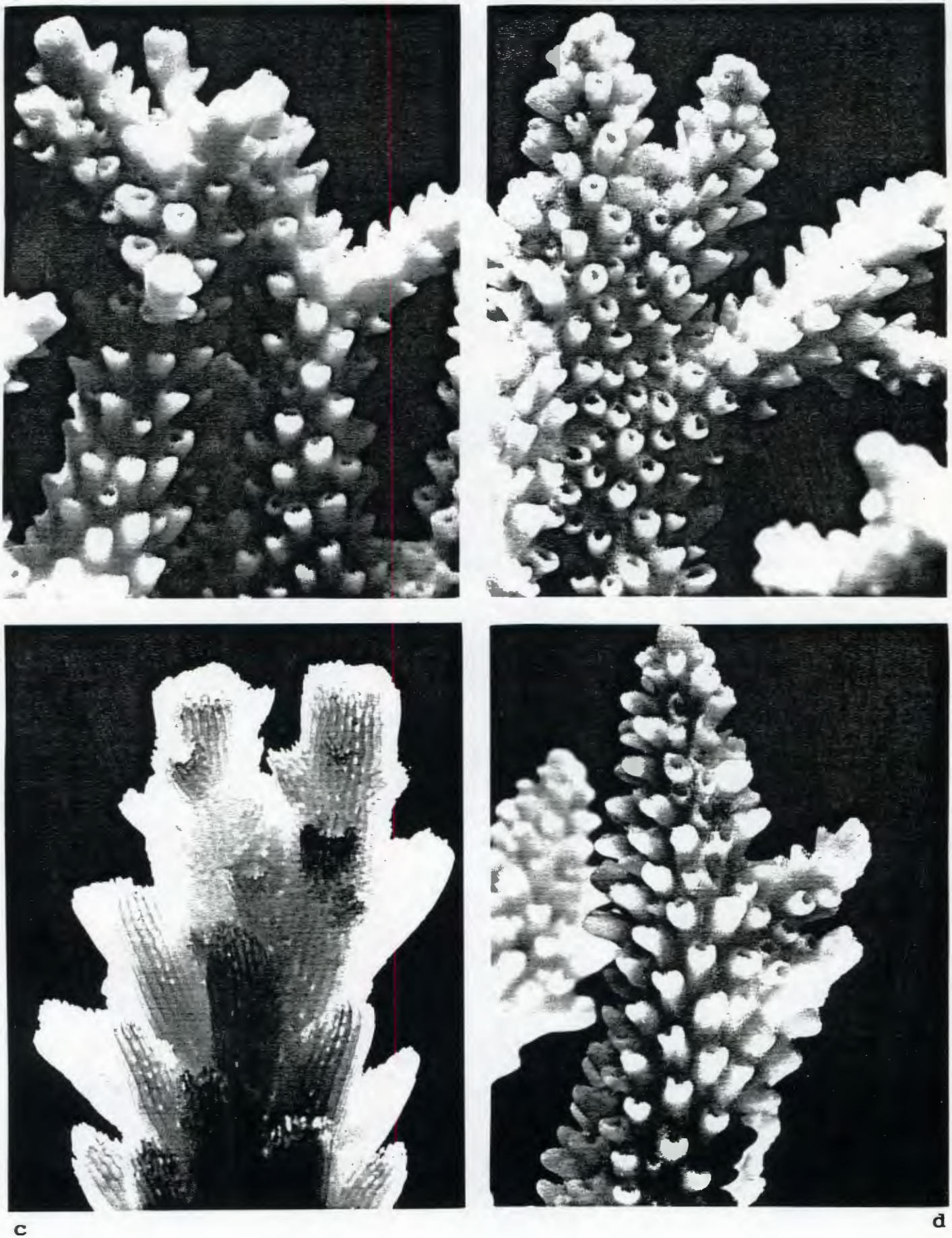
A) Acropora (Acropora) natalensis, SAM-H-4631, from 4-Mile Reef, Central Reef Complex, South Africa, x2.5.

B) Acropora (Acropora) natalensis, ORI/AIC7(2), from Pta. Torres, Inhaca Island, Mozambique, x2.5.

C) Acropora (Acropora) natalensis, SAM-H-4631, from 4-Mile Reef, Central Reef Complex, South Africa, x7.5.

D) Acropora (Acropora) natalensis, ORI/AlC7(2), from Pta.Torres, Inhaca Island, Mozambique, x2.5.

Plate 2 a, b, c & d



Radial corallites:

Of very inconsistent shape; near the tips tubular appressed with elongate to nariform opening; further down the branches most corallites are nariform; on horizontal parts of the branches most are nariform, sub-immersed to immersed; on the underside of the branches there are only a few very appressed tubular or subimmersed corallites. **Septation:** development varies, very reduced in most tubular corallites, where only the directive septum is showing, one cycle of septa may be present in form of spines (SAM-H-4630, ORI/A1C7(3))or developed to a size of 1/8-1/4 calyx radius (ORI/KB/1991-9-37, ORI/S5/1991-9-38); when one complete cycle is present, the second cycle often only shows as a row of spines (SAM-H-4631); the Holotype shows all these possible variations; on immersed, hooded corallites one to two cycles present, the septa of the second cycle however very small to completely absent.

Thecae and Coenosteum:

On the corallites costate to broken costate or rows of spinules which partially fuse to form broken costae, coenosteum covered with spinules, sometimes spongy; walls of radials can be fenestrate (ORI/S5/1991-11-12).

Observations:

The specimens used to describe this species form quite a heterogenous series but are held together by their growth form, the characteristics of their corallites and the coenosteum. All these characters place the species into the Acropora divaricata group (Veron & Wallace, 1984). Within this group it shows affinities to A.solitaryensis Veron & Wallace, 1984 and A.

stoddarti Pillai & Scheer, 1976. A.natalensis does not have regularly nariform radials on branchlets as A.stoddarti has. They are mostly tubular appressed throughout the branches and do not become immersed as in A. solitaryensis. Even on the horizontal branches the corallites are either nariform or tubular in A. natalensis, this is not the case in A.solitaryensis, where they are immersed on the lower parts of the branches (Veron & Wallace 1984). This species is very variable.

The colour of the living animals is always a deep chocolate-brown.

ETYMOLOGY: This species is named after the South African Province Natal, within which all South African reef-coral communities are situated.

ACROPORA (ACROPORA) SORDIENSIS sp.nov.

HOLOTYPE: SAM-H-4632 from 14m on Two-Mile Reef (27°30'S, 32°41'E), Central Reef Complex, Natal, South Africa; an entire colony, 200mm greatest diameter, 110mm greates height; collector B. Riegl.

PARATYPES: SAM-H-4633 from 21m on Four-Mile Reef (27°30'S, 32°41'E), Central Reef Complex, Natal, South Africa; entire colony, 145mm greatest diameter, 110mm greatest height; collector B. Riegl.

SAM/H-4634 from 14m on Two-Mile Reef (27°31'S, 32°41'E), Central Reef Complex, Natal, South Africa; entire colony, 115mm greatest diameter, 90mm greatest height; collector B.Riegl.

SAM-H-4635 from 12m on Two-Mile Reef (27°31'S, 32°41'E), Central Reef Complex, Natal, South Africa; entire colony,

Plate 3

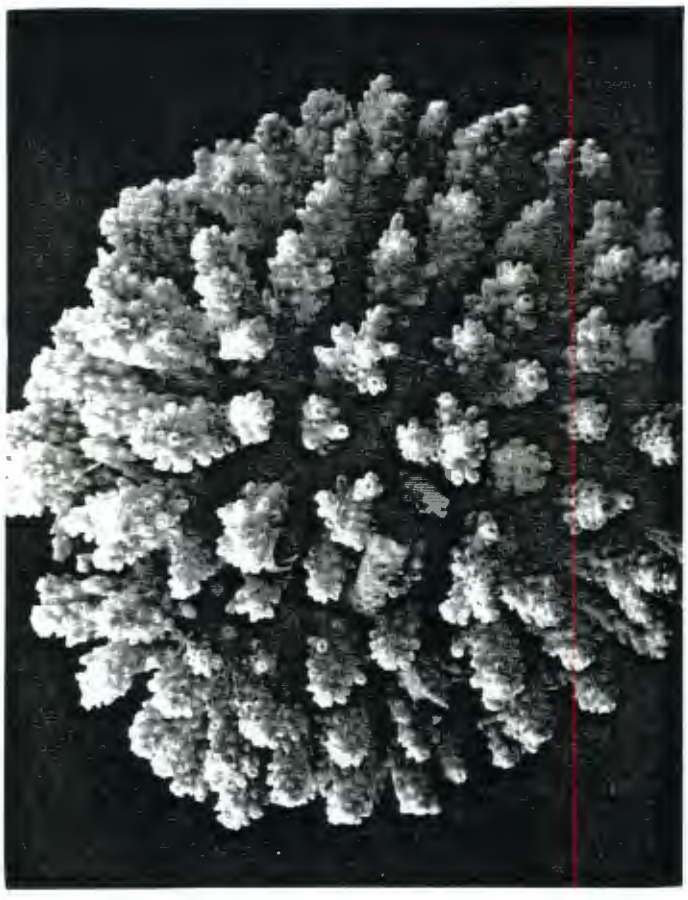
A) Acropora (Acropora) sordiensis, SAM-H-4632, Holotype, from 2-Mile Reef, Central Reef Complex, South Africa, x0.4.

B) Acropora (Acropora) sordiensis, SAM-H-3634, from 2-Mile Reef, Central Reef Complex, South Africa, x0.4.

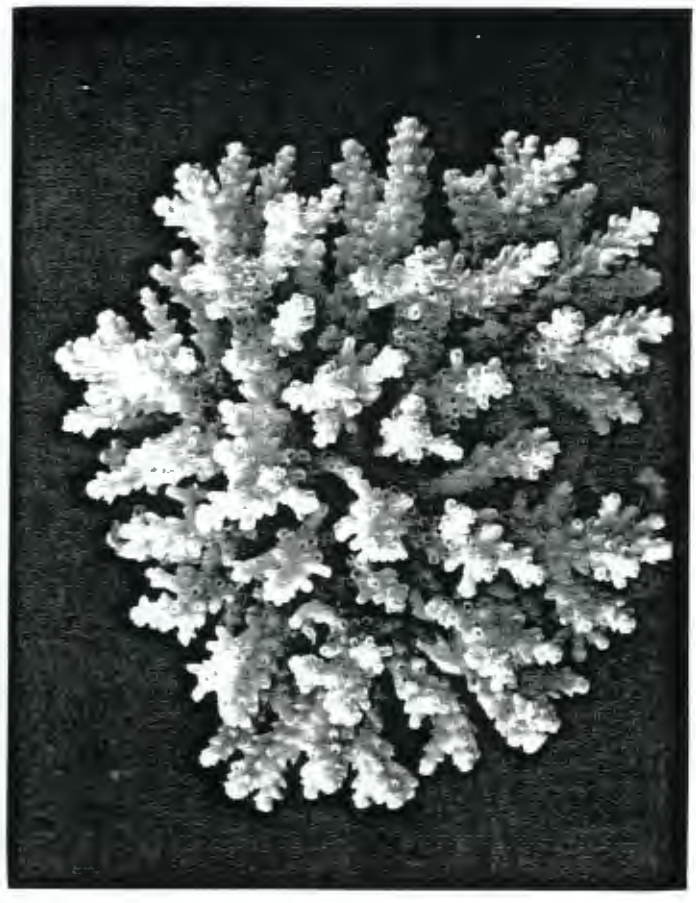
C) Acropora (Acropora) sordiensis, ORI/S9/1991-1-7, from 9-Mile Reef, ORI/S2/1991-7-12 from 2-Mile Reef in the Central Reef Complex, ORI/KB/1991-9-23 from the Northern Reef Complex off Kosi Mouth, South Africa, x0.3.

Plate 3 a, b & c

a



b



c

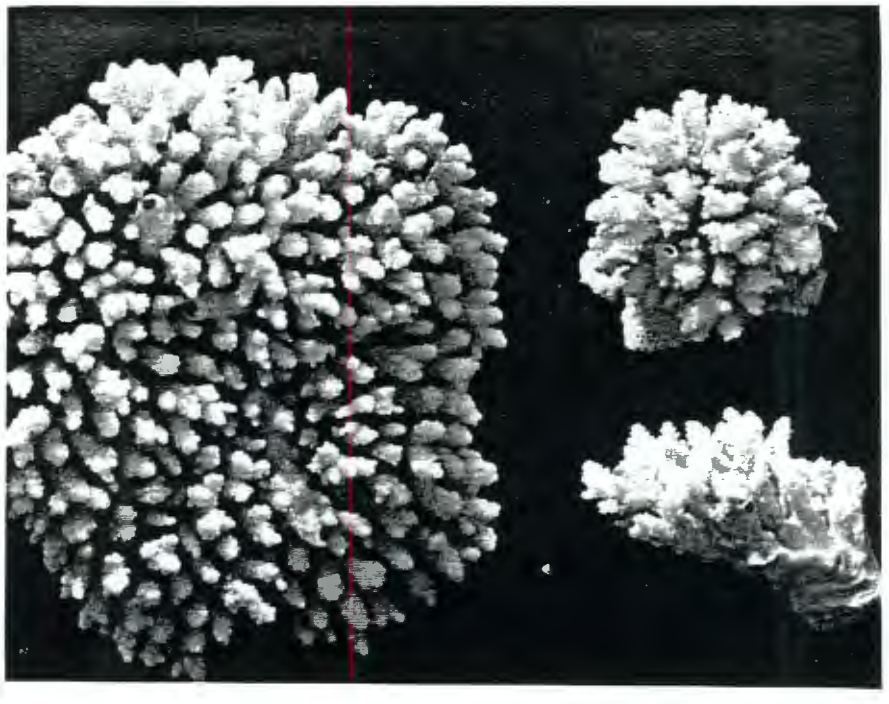


Plate 4

A) Acropora (Acropora) sordiensis, SAM-H-4636, from the Northern Reef Complex off Kosi Mouth, South Africa, x10.

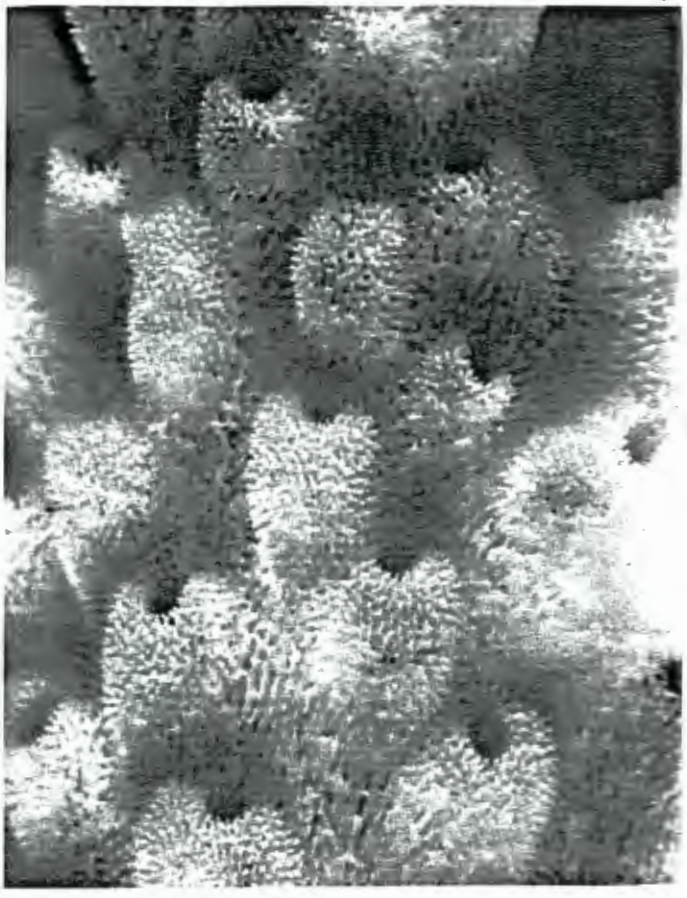
B) Acropora (Acropora) sordiensis, SAM-H-4636, from the Northern Reef Complex off Kosi Mouth, South Africa, x10.

C) Acropora (Acropora) sordiensis, ORI/S9/1992-1-7, from 9-Mile Reef, Central Reef Complex, South Africa, x1.

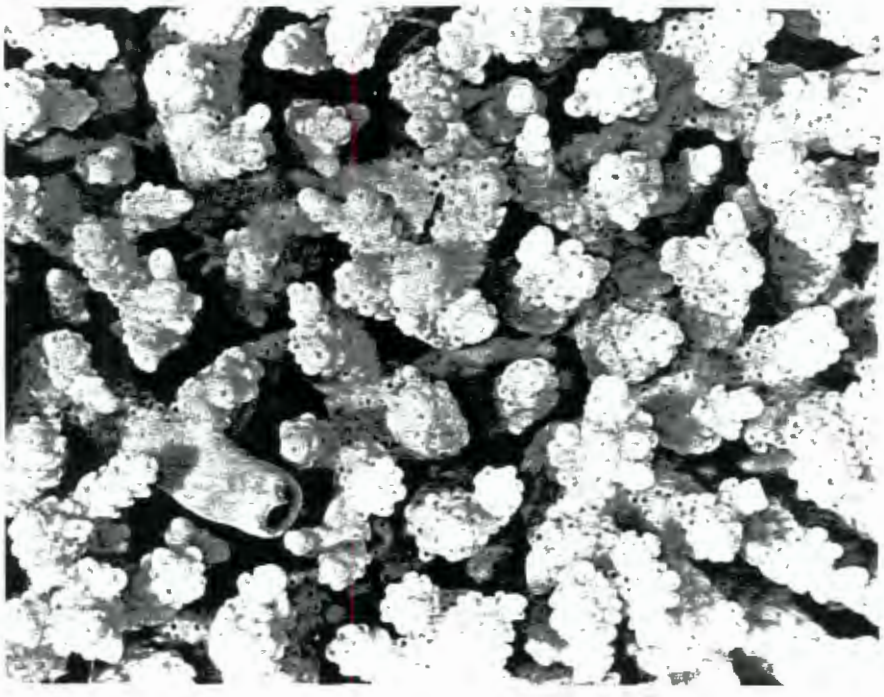
Plate 4 a, b & c

a

b



c



110mm greatest diameter, 75mm greatest height; collector B.Riegl.

SAM-H-4636 from 21m on Kosi-Mouth Reef (26°50'S, 32°38'E), Northern Reef Complex, Natal, South Africa; fragments of a colony; collector B. Riegl.

SAM-H-4637 from 15m on Two-Mile Reef (27°31'S, 32°41'E), Central Reef Complex, Natal, South Africa, entire colony; collector B. Riegl.

ORI/S9/1992-1-7 from 14m on Nine-Mile Reef (27°26', 32°40'E), Central Reef Complex, Natal, South Africa; entire colony, 255mm maximum diameter, 125mm maximum height; collectors B. Riegl and M. Schleyer.

Further specimens:

6 specimens from Two-Mile Reef, Central Reef Complex, South Africa (ORI/S2/1991-7-12, ORI/S2/1992-1-8, ORI/S2/1992-1-9, ORI/S2/1992-1-10, ORI/S2/1992-1-11, ORI/S2(/1992-1-12) 1 specimen from the Northern Reef Complex off Kosi Mouth, Natal, South Africa (ORI/KB/1991-9-23).

DESCRIPTION

Branching Pattern:

Caespito-corymbose, from a central attachment a heavy base of up to several centimetres thickness in large colonies is formed; branches are thick (7.5-11mm at the tips, 18-30mm at the bases) and terete to mildly tapering; in species from protected habitats branches are thinner, especially at their bases; growth orientation in all branches is upward, the lateral branches showing a tendencay to fuse in their basal parts, resulting in a bowl-shaped appearance of large colonies (ORI/S9/1992-1-7); at the branch bases are numerous long, ascending corallites the

transition of which into thin branchlets is easily visible in older colonies (Holotype and ORI/S9/1992-1-7); at the tips of the branches numerous incipient axials and scondary branchlets are found, often more than two per branch, which gives the branch arrangement an irregular appearance.

Axial corallites:

Very irregular in shape and size, always conspicuous, conical, tapering from 3.2-6.5mm at the base to 2.5-6.0mm at the tips; exsert by 1.9-4mm; calyx diameter 1.1-2.3mm, often laterally compressed, resulting in an elongate calyx. In some instances, in particularly large axials, a second calyx is being formed by a process resembling intratentacular budding of the axial (ORI/S2/1991-9-8, ORI/S9/1992-1-7). **Septation:** well developed, mostly in two cycles (first cycle:1/4-1/2 calyx radius, second cycle 1/8-1/4 calyx radius) with prominent directive septa (3/4-2/3 calyx radius), in individual large corallites a third cycle may be developed; in large corallites septa are markedly dentate, especially deep inside the calyx, septal dentations are however absent in most smaller calices.

Radial corallites:

Mostly appressed tubular with round to nariform opening. The inner (upper) corallite wall is often absent, therefore the outer (lower) wall forms a lip, which is pointed and hook-like; some ascending tubular radials with dimidiate openings are present near the tips of the branches; near the bases of the branches most corallites become sub-immersed to immersed, near the bases and the tips of the branches numerous incipient axials are developed. On coralla from sheltered environments (SAM-H-4634) radials are less

appressed, the inner (upper) wall is better developed; corallites then often have nariform openings or become fully tubular with oval to round openings. **Septation:** mostly only one cycle (1/8 calyx radius) with prominant directive septa (1/4 calyx radius), second septal cycle only present as a low ridge.

Thecae and Coenosteum:

Walls are thick and covered by a dense arrangement of laterally flattened, elaborate spines, which are arranged in rows; despite their apparent thickness, the walls can be very spongy (ORI/S9/1992-1-8); the coenosteum is reticulate with spinules and also very spongy in appearance.

Observations:

The structure of the axial corallites and the thickset branches would put this species somewhere close to the Acropora humilis group (Veron & Wallace, 1984). The structure of the radial corallites however does not suggest this grouping. The most logical grouping for this species seems to be the Acropora lovelli group (Veron & Wallace, 1984), within which A. sordiensis is closest to A. verweyi Veron & Wallace, 1984. This closeness is based on coenosteum characteristics and the shape of the radial corallites. However, A. sordiensis has a much more regular growth pattern and thicker, shorter branches than A.verweyi. Species within the A. lovelli group are defined to "...have some resemblance to each other or to species of the A. humilis group..." (Veron & Wallace, 1984). It is a very heterogenous grouping of species, which do not fit anywhere else. The absence of an upper wall in many radial corallites of A. sordiensis is reminiscent of the situation in A. digitifera. However, the

species differ greatly in the shape and arrangement of the radial corallites. A missing upper wall is typical of the A. aspera group (Veron & Wallace, 1984), but the species in this group have a different branching pattern and different coenosteal characteristics.

The coulour of the living animal ranges from brown to yellow and green with blue branch tips. This species is common on South African reef systems but has not been recorded elsewhere.

Etymology: Named after Sodwana Bay in the Central Reef Complex, South Africa. The area is often colloquially referred to as "Sordies", from which the name is derived.

ACROPORA (ACROPORA) MOSSAMBICA sp.nov.

HOLOTYPE: ORI/A1C1(4) from Xai Xai, Mozambique (25°8'S, 33°42'E) intertidally on rocks; collector P. Boshoff; an entire colony, maximum length 75mm, maximum width 65mm, maximum height 45mm.

PARATYPES: ORI/A1C1(1) from Cabo da Inhaca, Inhaca Island, Mozambique (26°10'S, 32°30'E); intertidally; collector P.Boshoff.

ORI/A1C1(2) from Baixo 213, Inhaca Island (26°10'S, 32°30'E), Mozambique, subtidally; collector P.Boshoff.

ORI/A1C1(3) from Umdloti, Natal, RSA (30°32'S, 31°12'E), intertidally; collector P.Boshoff.

ORI/A1C18(1) from Pta. Torres, Inhaca Island, Mozambique (26°10'S, 32°30'E), collector P. Boshoff.

ORI/A1C18(2) from Pta. Rasa, Inhaca Island, Mozambique (26°10'S, 32°30'E); collector P. Boshoff.

Plate 5

A) Acropora (Acropora) mossambica, ORI/A1C1(4), Holotype, from Xai Xai, Mozambique, x3.

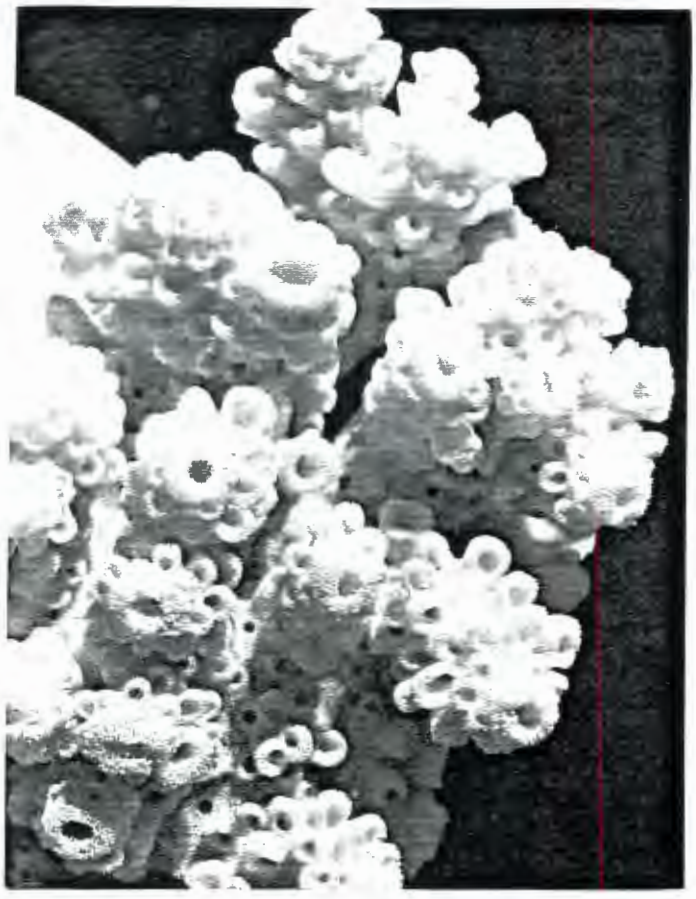
B) Acropora (Acropora) mossambica, ORI/A1C18(1), from Pta. Rasa, Inhaca Island, Mozambique, x2.

C) Acropora (Acropora) mossambica, ORI/A1C1(3), from Umdloti, Natal North Coast, South Africa, x1.

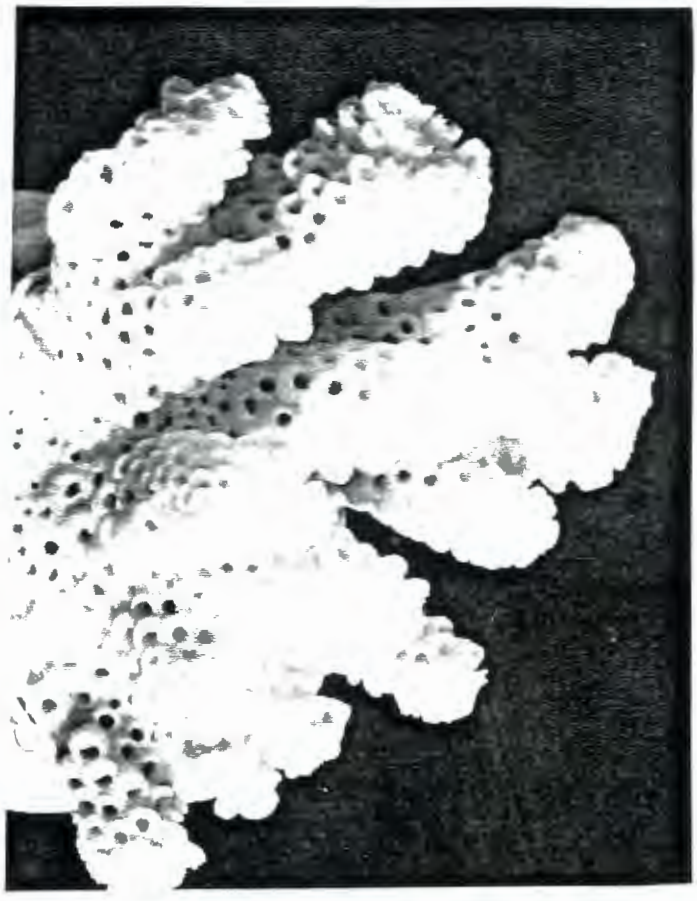
D) Acropora (Acropora) mossambica, ORI/A1C1(3), from Umdloti, Natal North Coast, South Africa, x3.

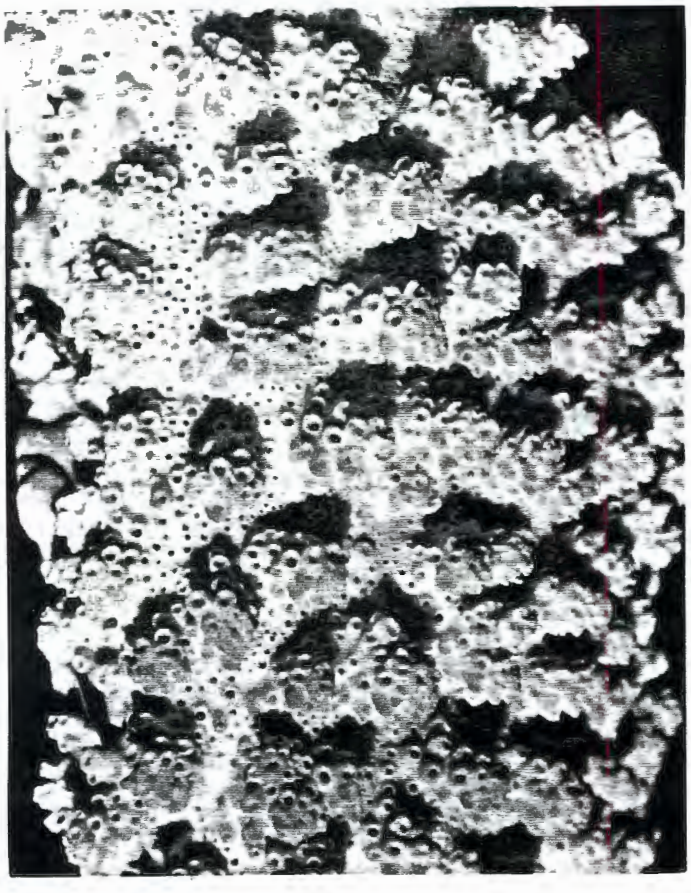
Plate 5 a, b, c & d

a

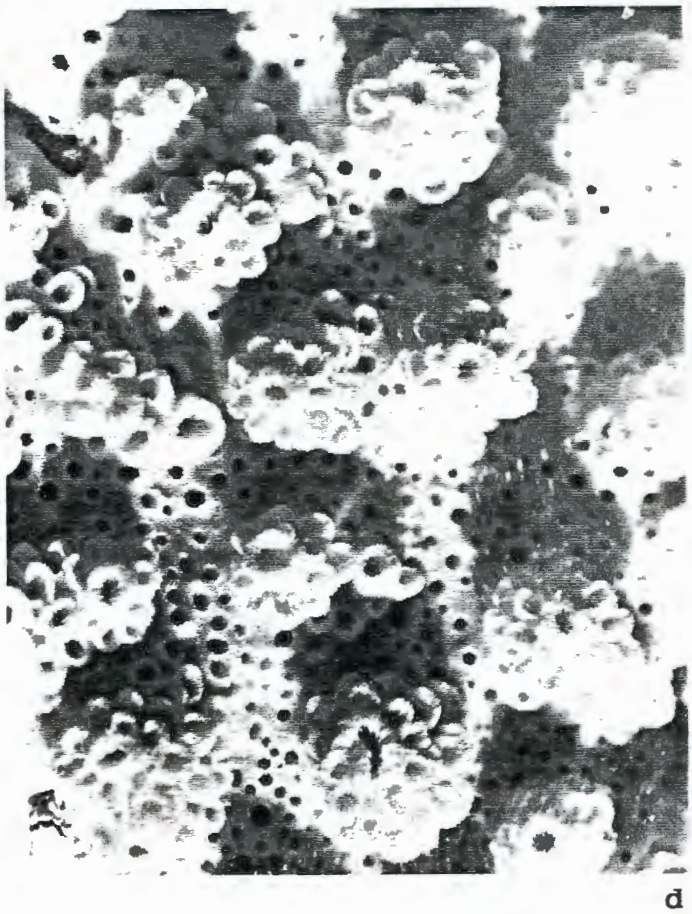


b





c



d

Plate 6

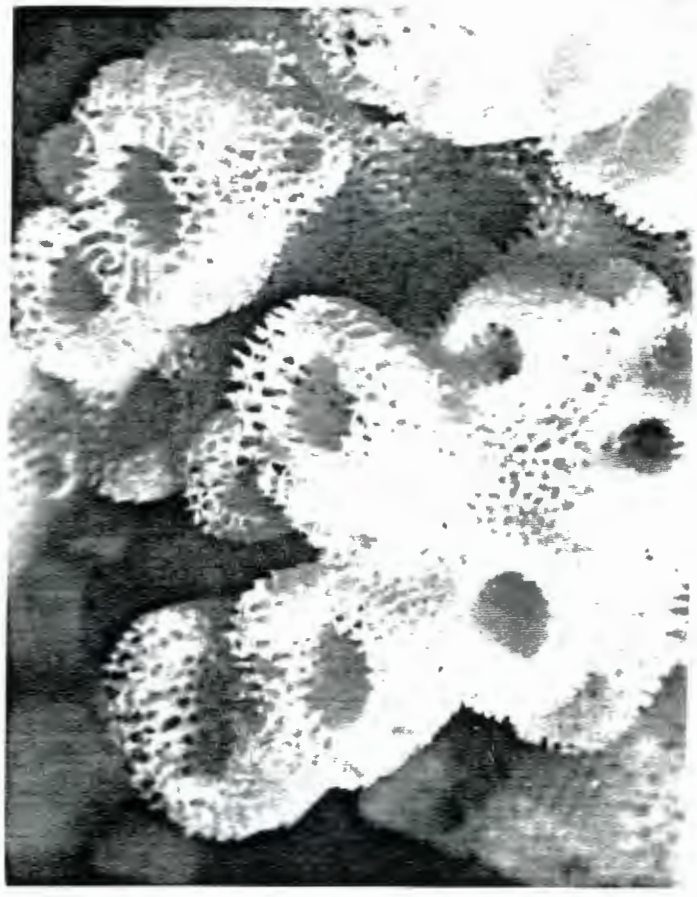
A) Acropora (Acropora) mossambica, ORI/AlCl(4), Holotype, axial corallite, x10.

B) Acropora (Acropora) mossambica, ORI/AlCl(4), Holotype, radial coralliutes, x10.

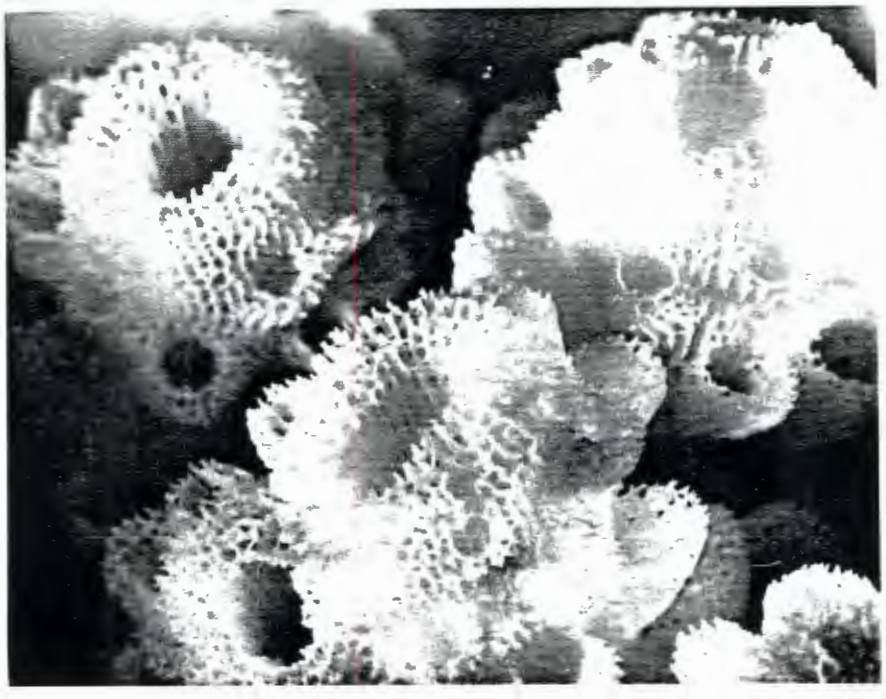
D) Acropora (Acropora) mossambica, ORI/Alc1(4), Holotype, axial corallites, x10.

a

b



c



DESCRIPTION

Branching Pattern:

Low, bushy to corymbose, with little secondary branching; a continuous basal plate can be developed, which shows a tendency to grow outward and upward. This has lead to the corallum of ORI/AlCl(3) being more massive than truly branching. The plate is the result of filling between the upward arching horizontal branches on ORI/AlCl(3). On most specimens there is relatively little true horizontal branching, only the branches on the edge of the colony are oblique, but with a strong upward growth tendency (as on ORI/AlCl(3), ORI/AlCl(4), ORI/AlC18(1), ORI/AlC18(2)).

Axial corallites:

Very conspicuous, cylindrical with a very thick but porous wall, moderately to hardly exsert (up to 2mm), outer diameter 3.3-5.7mm, calyx diameter 1.1-3.4mm, characteristically laterally compressed, in most axials the calyx is not round but elongate. Septation: moderate to weak development in the distal part of the calyx (1/8-1/2 calyx radius, sometimes only visible as low ridges), septa becoming bigger further down the calyx (1/2 -1/3 calyx radius) where they bear spines; the directive septa meet at the bottom of the calyx and are bigger than the others. Two septal cycles present, the first cycle is always twice the size of the second cycle.

Radial corallites:

Tubular through appressed tubular to nariform near the tips of the branches, becoming increasingly smaller further down the branches; on the bases of the branches and on the basal plate mainly sub-

immersed and immersed corallites. Corallite arrangement on the branches is irregular with large corallites having a tendency to proliferate and turn into incipient axials; corallite diameter 2.5-3.4mm, the lower (outer) wall better developed, often also lipped, the lip being rounded and flaring, sometimes hook-like. **Septation:** in general poorly developed with only the directive septa showing, the outer directive septum being better developed than the inner one; on incipient axials and certain large radials septa are well developed with two cycles and prominant directives; in some corallites no septa at all. Septa are best developed in ORI/AlC1(3) where two septal cycles are present (first cycle:1/4 calyx radius, second cycle 1/8 calyx radius); in immersed corallites on the basal plate usually only one septal cycle present (1/8 calyx radius).

Thecae and Coenosteum:

Walls are very porous despite their apparent thickness, some are fenestrate (on ORI/AlC18(1) and ORI/AlC18(2)); the coenosteum is costate to broken costate on the corallites, on the basal plate a dense arrangement of spinules gives a spongy appearance.

Observations:

A.mossambica superficially shows some resemblance to A.tenuis, of which it looks like an oversized version. It differs from A.tenuis by the much larger size of its corallites, especially the axials. The structure of the radials, compressed with rounded calyces and flaring outer wall, is also similar to A.tenuis, however not showing the usually neat arrangement of this species. The growth form of A.mossambica could be considered to be an extreme variation of a basically corymbose branching pattern.

The structure of the radial corallites would place A.mossambica within, or at least near, the Acropora selago group (Veron & Wallace, 1984), which is characterized by having "...similar radial corallites with strongly developed lower walls and flaring or pointed lower lips..." (Veron & Wallace, 1984).

There is also a similarity to Acropora macrostoma (Brook, 1891), as illustrated and discussed by Brook (1893). However, Brook's A.macrostoma is a corymbose, tabular specimen, whereas the present specimens are far from any tabular condition as they are very small. It cannot be excluded with certainty that under favourable environmental conditions typically corymbose plates would be formed. But judging from the present specimens and their typical intertidal or infratidal habitat this seems unlikely.

A.mossambica occurs in South East Africa in permanent tidal pools, sometimes sharing them with another intertidal species, A.branchi (see below). The colour of the living animal is pale sand-coloured to light brown.

ETYMOLOGY: Named after the South East African country Mozambique, where this species was first collected.

ACROPORA (ACROPORA) BRANCHI sp.nov.

SYNTYPES: SAM-H-4620 from a tidal pool at Chaka's Rock (30°31'S, 31°13'E), Natal, South Africa, an entire colony attached to a rock, greatest length 110mm, greatest width 65mm, greatest height 75mm, collector B.Riegl.

SAM-H-4621 from tidal pool at Chaka's Rock (30°31'S, 31°13'E), Natal, South Africa, fragment of a massive colony, greatest

length 130mm, greatest width 140mm, greatest height 85mm, collector B.Riegl.

PARATYPES: SAM-H-4622 from tidal pool at Chaka's Rock (30°31'S,31°13'E), Natal, South Africa, collector B.Riegl.

SAM-H-4623 from tidal pool at Chaka's Rock (30°31'S, 31°13'E), Natal, South Africa, collector B.Riegl.

SAM-H-4624 from tidal pool at Chaka's Rock (30°31'S, 31°13'E), Natal, South Africa, collector B.Riegl.

SAM-H-4625 from tidal pool at Chaka's Rock (30°31'S, 31°13'E), Natal, South Africa, collector B.Riegl.

SAM-H-4626 from tidal pool at Chaka's Rock (30°31'S, 31°13'E), Natal, South Africa, collector B.Riegl.

SAM-H-4627 from tidal pool at Chaka's Rock (30°31'S, 31°13'E), Natal, South Africa, collector B.Riegl.

SAM-H-4628 from tidal pool at Chaka's Rock (30°31'S, 31°13'E), Natal, South Africa, collector B.Riegl.

ADDITIONAL SPECIMENS: ORI/A1C26(1) from Chaka's Rock, Natal.

ORI/A1C26(1) from Pta.Zavora, Mozambique.

ORI/A1C19(1) from Unhlanga Rocks, Natal.

DESCRIPTION

Branching Pattern:

Extremely variable, from incrusting through low, bushy corymbose to massive; the basic branching pattern is corymbose (SAM-H-4621) but the incrusting basal area, which in most specimens stretches far beyond the upward branching area, shows a tendency to grow upward, which then leads to a fusion of the bases of the short branches. This situation may go so far, that no true branches are developed and only the entire basal plate grows upward to form a massive colony with only very short branchlets, which are little

Plate 7

A) Acropora (Acropora) branchi, SAM-H-4621, Syntype, a small, branching colony from a very sheltered location in a tidal pool at Chaka's Rock, Natal North Coast, South Africa, x1.

B) Acropora (Acropora) branchi, SAM-H-4622, a small, branching colony, from a sheltered location in a tidal pool at Chaka's Rock, Natal North Coast, South Africa, x1.

C) Acropora (Acropora) branchi, ORI/A1C26(1), a branching colony, showing fusion of lateral branches into a plate, from Chaka's Rock, Natal North Coast, RSA.

D) Acropora (Acropora) branchi, SAM-H-4620, Syntype, peripheral part of a large, massive growing colony on the seaward edge of an intertidal rock-platform at Chaka's Rock, Natal North Coast, South Africa, x0.5.

Plate 7 a, b, c & d

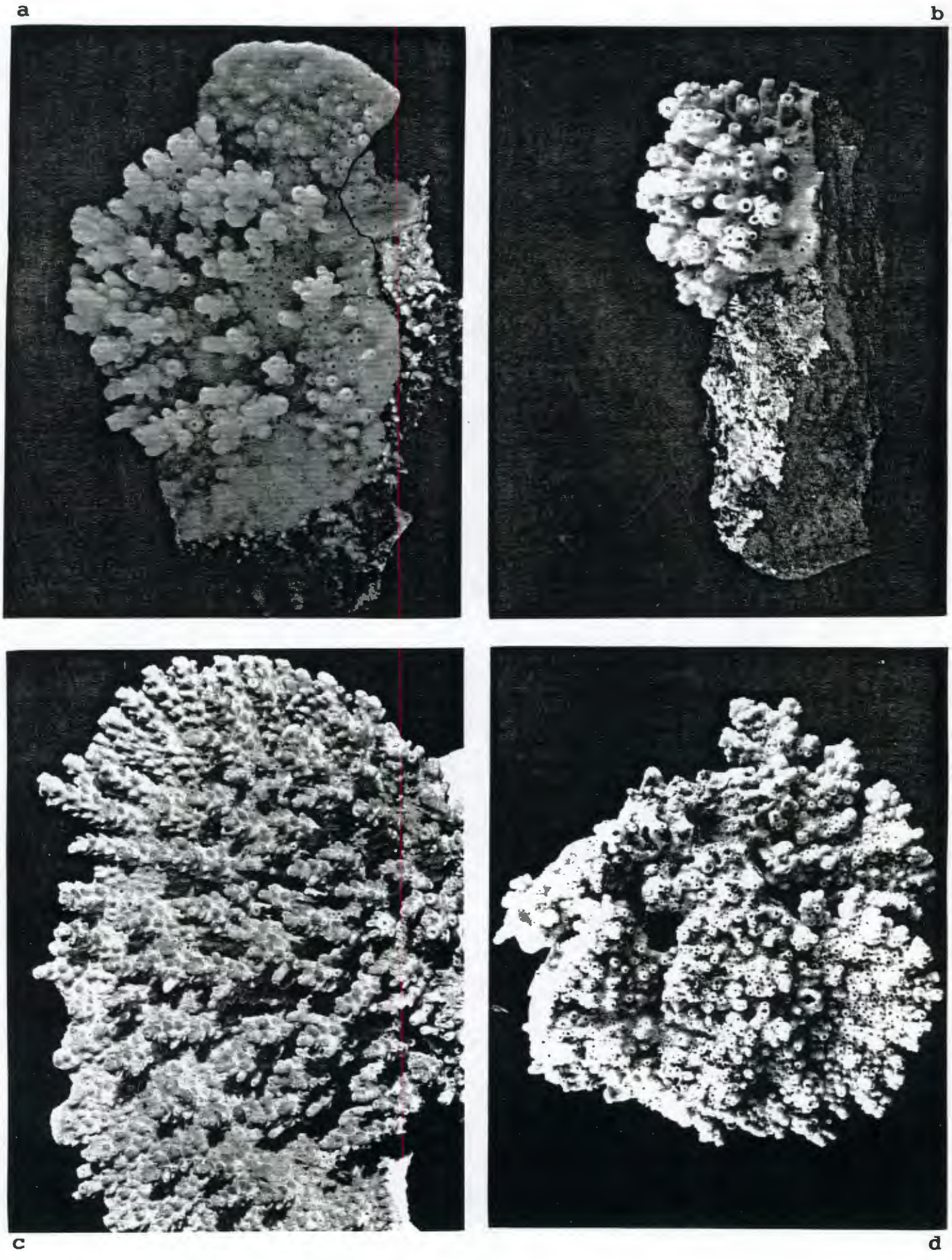


Plate 8

A) Acropora (Acropora) branchi, SAM-H-4628, part of the laminar edge of a massive colony, from Chaka's Rock, Natal North Coast, South Africa, x1.

B) Acropora (Acropora) branchi, SAM-H-4627, part of a massive colony with no branching, from the wave-exposed edge of an intertidal rock platform at Chaka's Rock, Natal North Coast, South Africa, x2.

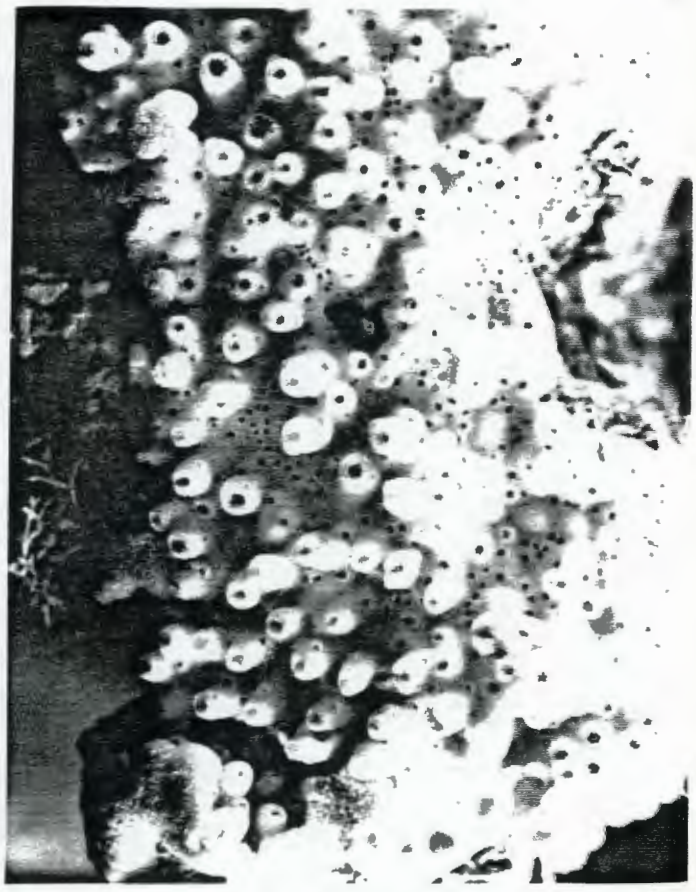
C) Acropora (Acropora) branchi, SAM-H-4621, an enlarged branchlet, showing the coenosteum, specimen from Chaka's Rock, Natal North Coast, South Africa, x5.

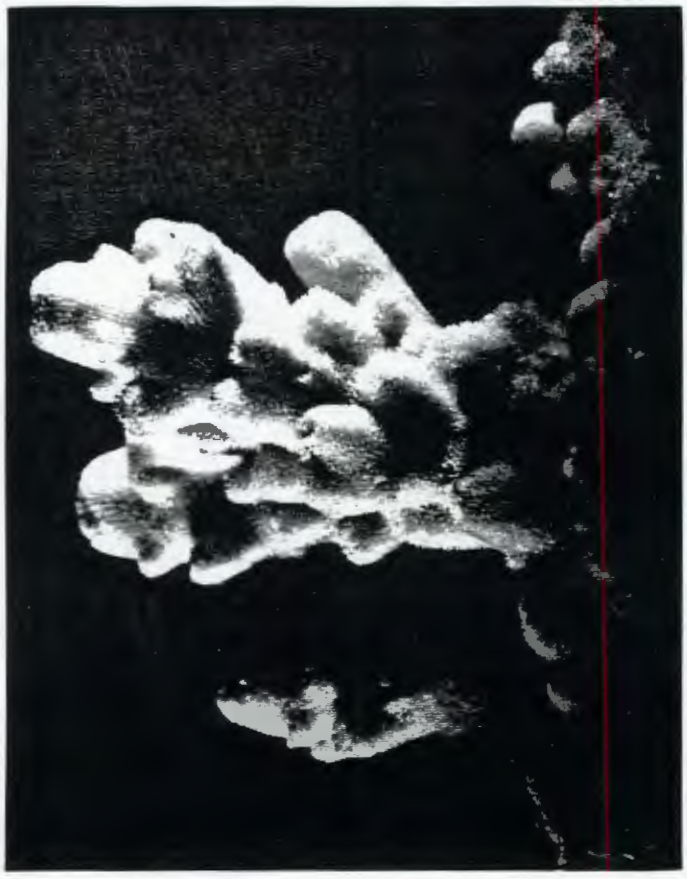
D) Acropora (Acropora) branchi, SAM-H-4621, immersed corallites on the incrusting basal plate of this specimen, from Chaka's Rock, Natal North Coast, South Africa, x10.

Plate 8 a, b, c & d

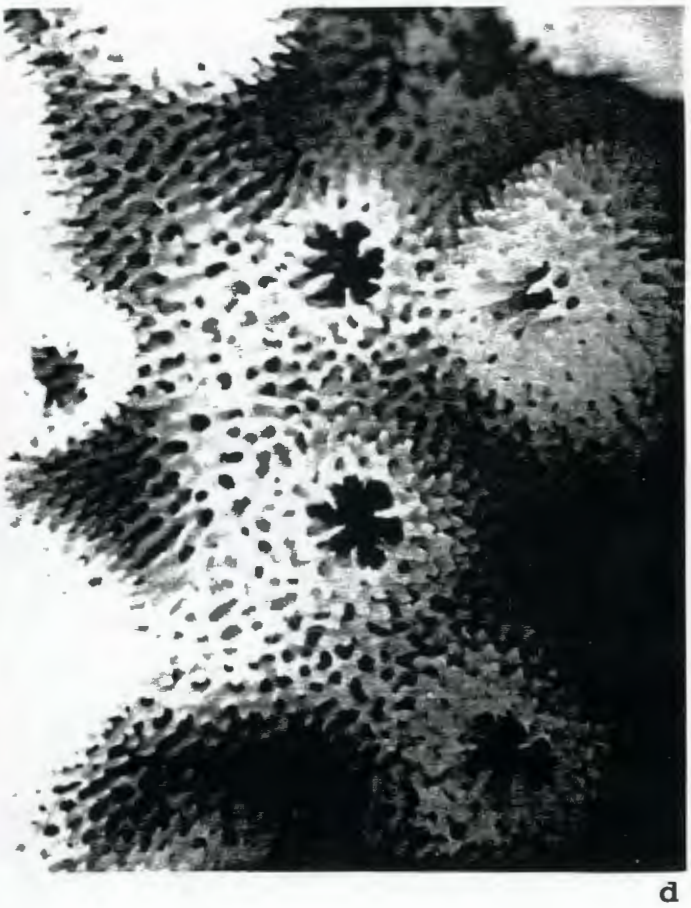
a

b





c



d

more than incipient axials, protruding from its surface(SAM-H-4620). The lateral extension of the colony happens by fusion of branches, which then form plates much like in A. clathrata (Brook, 1891). The growth direction is determined by single axial corallites, wherever present, so that this species has to be grouped with the subgenus Acropora.

Axial corallites:

Mostly cylindrical but some markedly conical, usually hardly or not at all tapering; outer diameter from 2.4-4mm, hardly to well exsert (1-2.5mm), calyx diameter 0.8-2.6mm, in some specimens the larg axial corallites are laterally compressed, thus having elongate calyces, size of axials may vary greatly within the same colony, on the growing edge of platelike lateral parts adjacent axials sometimes fuse. Septation: depending on the size of the calyx one to two septal cycles developed (in small calyces only one cycle or the second cycle only visible as a low ridge), septa are dentate, size 1/4-1/3 calyx radius, directive septa usually larger 1/3-1/2 calyx radius. Septa increase in size deep in the calyx, where one directive septum may increase to size 2/3 of calyx diameter.

Radial corallites:

On branches, tubular to tubular appressed usually with a round opening, on some specimens developing a hooked, rounded lip. Size very variable, but mostly about half the size of the axial corallite, diameter 1.4-2.2mm, calyx diameter 0.9-1.1mm. Towards the bases of the branchlets (where developed) radials become more appressed; size, shape and distribution of radials over the branches is very irregular. On the basal, massive part of the

skeleton numerous immersed corallites of very irregular size and distribution. Tiny corallites ore often densely packed, especially between branches or tall incipient axials; these corallites are only half the size of the normal immersed corallites (calyx diameter of normal corallites 0.9-1.0mm); on some specimens sub-immersed hooded corallites or even tubular appressed corallites on the basal part of the corallum pare resent; at irregular intervals tubular corallites are exsert by up to 4mm, most of which seem to turn into incipient axials. **Septation:** Always one complete cycle (size 1/8-1/4 calyx radius, in larger corallites often two complete cycles , the second cycle only 1/4 or 1/2 the size of the first cycle and often only developed 0.5-1mm away from the upper edge of the calyx, larger septa are dentate, directive septa are only slightly larger than others.

Thecae and Coenosteum:

Covered with fine, elaborate spinules which may or may not be arranged in rows; if arranged in rows, partial fusion is often observed. On the basal part the appearance of the coenosteum is spongy.

Observations:

The growth form, very low pseudo-corymbose branching with massive infilling between the basal parts of the branches caused by an upward growing basal area, is very similar to that observed in A.mossambica. The completely different corallite, coenosteal and thecal structure seperates these species very well. In A.mossambica branches are formed regularly in all available specimens, even if they are only very short and blunt. In A.branchi, however, upward pointing branches are only formed in

specimens from extremely sheltered habitats; in most specimens no branches are formed. The fused lateral branches, on the growing edge of the corallum, show in their structure certain similarity to those observed in South African specimens of A.clathrata (Brook, 1891). It seems possible, that some relationship exists between these species, which would also be suggested by similar corallite and coenosteal structures. A.clathrata (Brook, 1891) is grouped within the A.divaricata group (Veron & Wallace, 1984). This group is held together by "...similar nariform to tubo-nariform radial corallites and a similar coenosteum...". This definition however excludes A.branchi sp. nov. from this group, as this species' corallites are typically tubular. The most logical grouping for this species would be the A.loripes group (Veron & Wallace, 1984), being held together by "...an essentially similar very fine coenosteum, giving a smooth appearance similar to the coenosteum of the Dendrophylliidae..." (Veron & Wallace, 1984). Within this group, radial corallites are very variable but mostly tubular.

ETYMOLOGY:

This species is named after George and Margo Branch of the University of Cape Town, who first discovered this species, in recognition of their contribution to South African and my own marine science.

AN IDENTIFICATION KEY TO THE HARD CORAL GENUS ACROPORA Oken, 1815 IN SOUTH EAST AFRICA

This key is intended to provide easily discernible clues in order to allow quick identification of the local species of Acropora. Therefore it centers its approach on the most obvious characters of the corals, their growth-form. On a broader geographic scale this approach may be problematic because particularly in Acropora, growth form can vary extremely, given different environmental conditions. In South East Africa however, and particularly in South Africa, coral reefs offer very uniform environments because there is very little geomorphological differentiation of the substratum (see Part II, Chapter 1) and corals tend to have very uniform growth forms across the described range. It is therefore possible to use growth form as a first differentiating tool. This makes the key easier to use and makes preliminary identification possible far from the laboratory. Appropriate monographs should however be consulted to verify the identifications.

1 Branches with only one clearly differentiated axial corallite at the end of each branch or the growing edge of plates.....2

1* Branches with more than one or no clearly differentiated corallites at the end of each branch, growth form massive with no branches at all or branching with wide, blunt or wedge-shaped branches.....A.palifera

2(1) Massive to submassive base with short branches.....3

2* Growth form different.....4

3(2) Growth form shows all transitions from massive with no branches through submassive with short branches to small corymbose clumps, branch diameter around 0.7 cm, axial corallites conical radials tubular to tubular appressed with round opening, in tidal pools.....A.branchi

3* Never massive without branches, always short, thick and terete, upwards directed branches present; also grows in small corymbose clumps, branch diameter 10-15 mm, axial corallites conical with thick, porous wall, often laterally compressed, radials appressed tubular to nariform, the lower wall better developed than the upper, in tidal pools.....A.mossambica

4(2*) Branches hispidose, covered on all sides or only on upper side with secondary branchlets, giving a "bottle-brush" appearance.....A. florida

4* Branches other than hispidose.....5

5(4*) Tabular to platelike, in South Africa always solid, vasiform plates.....6

5* Corymbose, ceaspito-corymbose, caespitose or arborescent..15

6(5) Colonies are solid, vasiform plates with little or no

vertical branchlets.....A.clathrata

6* Fully, or almost tabular, tables not fused to plates.....7

7(6*) Tabular, growing from a central or lateral attachment the horizontal growth component being more pronounced than the vertical; horizontal branches round or laterally compressed and anastomose irregularly..... 8

7* Tabular, but horizontal branches vertically compressed with frequent anastomoses; or vertical growth component more pronounced than horizontal growth component.....14

8(7*) Vertical branchlets fine and short (1-2 cm), projecting upwards with small corallites (1-2 mm diameter).....9

8* Vertical branchlets thicker and longer (1-3 cm), projecting upwards with medium sized corallites (2-3 mm diam.)....12

9(8) Branchlets and radials very uniform in shape and length....10

9* Branchlets and radials variable in shape and length.....11

10(9) Radial corallites neatly arranged in spirals along the branchlets, tubular to tubular appressed and labellate with dimidiate to nariform opening.....A.hyacinthus

10* Radial corallites not neatly arranged in spirals, tubular to tubular appressed, often labellate with dimidiate to nariform opening.....A.cytherea

11(9*) Branchlets composed of several axial corallites and their radials giving the branchlets an irregular appearance, large axials.....A.anthocercis

11* Radials very irregular, increasing in length towards the branch tip, mostly tubular with nariform to round opening.....A.paniculata

12(8*) Vertical branchlets thick and long, diameter 7-13 mm, length up to 90 mm, very regularly arranged, radials very

neatly arranged in spirals, appressed tubular with round to nariform opening, forming a "rosette".....A.tenuis

12* Vertical branchlets thinner and shorter, radials not forming a rosette.....13

13(12*) Vertical branchlets very regular and well spaced, length 1-3 cm, diameter 0.8-10 mm, radials arranged in rows, tubular appressed with round opening, walls not perforate, coenosteum with rows of spines.....A.latistella

13* Corallum similar, but branches thinner (up to 0.8 mm), radials wider spaced with thin, often perforate walls, coenosteum costate.....A.aculeus

14(7*) Tabular, horizotal branches noticeably flattened, colonies growing in single or double tiered colonies, horizontal branches typically flattened with numerous, irregular anastomoses, vertical branchlets very irregularly developed, radials mostly nariform or tubular with nariform opening.....A.natalensis

14* Caespito-corymbose showing a tendency to form a table with a long central stalk, the vertical growth component more pronounced than the horizontal, thin branches, radials tubular appressed to nariform, labellate to dimidiate.....A.cf.striata

15(5) Mostly corymbose, heavy structured with thick (10-30 mm) straight branches, radials usually neatly arranged in rows or spirals, axials very conspicuous.....16

15* Growth form different.....19

16(15) Branches short and stout, axial corallite small (slightly bigger than radials), most corallites of about the same size, tubular with round opening.....A.monticulosa

16* Branches different.....17

17(16*) Branches long, often of variable length, slightly to strongly tapered, conspicuous and well exsert axial (3-4 times the size of radials), radials with well developed upper wall, secondary branchlets only arising from lower part of main branches.....A.humilis

17* Branches, axials and radials different.....18

18(17*) Branches thick and tapering, 2 types of radials (immersed and tubular), axial smaller than in the previous species (2-3 times the size of the radials).....A.gemmifera

18* Branches thin (around 10 mm), short, axial conspicuous (twice the size of radials), radials with weakly developed upper wall, branchlets given off in all parts of the main branches.....A.digitifera

19(15*) Corymbose and heavy structured with conspicuous axials, irregular in size and shape, often compressed; radials never neatly arranged in rows or spirals, tubular appressed to immersed, with round or labellate opening.....A.sordiensis

19* Growth form and thickness of branches different.....20

20(19*) Corymbose and slender branches of uniform shape and appearance; or not corymbose at all.....24

20* Corymbose to tabular with medium thick branches.....21

21(20*) Thickset to slender branches, conspicuous axials, radials neatly arranged in rows and spirals, upper wall of radials always missing, lower wall developed as a lip.....A.millepora

21* Structure of radials different, always with upper wall.....23

22(21*) Corymbose to caespito-corymbose, radials typically

nariform, neatly arranged in spirals or rows, only on lower part of the branches immersed corallites.....A.nasuta

22* Arrangement or size of radials different.....23

23(22*) Corymbose to caespito-corymbose, radials tubular appressed, some with nariform opening, with sub-immersed corallites interspersed on all parts of the branches..A.valida

23* Similar growth form, radials not uniform in size and shape, sometimes alternating, long, tubular corallites are arranged in rows with interspersed immersed ones.....A.secale

24(20) Corymbose, very uniform long and slender, terete branches, radials widely spaced and tubular appressed to sub-immersed, very few incipient axials.....A.nana

24* Not corymbose.....25

25(24*) Bushy to arborescent, thick horizontal branches give off short branchlets, diameter up to several cm, often heavily calcified, radials of mixed sizes and shapes give the branches a ragged appearance.....A.danai

25* Open arborescent and sprawling.....26

26(25*) Numerous incipient axials and secondary branchlets along the main branches.....29

26* Very few to no incipient axials and secondary branchlets...27

27(26*) Radial corallites of irregular shape, tubular to immersed, long straight and sprawling branches with few subdivisions.....A.formosa

27* Radial corallites uniform.....28

28(27*) Radial corallites regularly and well spaced, tubular, tubular appressed to tubo-nariform; straight, slender, tapering branches.....A.microphthalma

28* Arborescent to bushy, radials irregularly spaced, tu-

bular, branches slender and tapering with irregular subdivisions.....A.horrida

29(26) Long sprawling branches with numerous incipient axials on the upper side, very few corallites on the lower side, radials vary from tubular to sub-immersed.....A.austera

29* Numerous secondary branchlets all over the upper side of the main branches leading in extreme cases to a hispidose growth form, radials tubular appressed.....A.florida

A REVISION OF THE HARD CORAL FAMILY FAVIIDAE Gregory, 1900 (SCLERACTINIA: FAVIINA) IN SOUTH EAST AFRICA

Abstract

This monograph describes all species of the hard coral family Faviidae, presently known to occur in South East Africa (i.e. the African mainland coast south of the Tropic of Capricorn and the Atoll Bassas da India in the Mozambique Channel. Most species are of wide Indo-Pacific distribution. The faviid fauna of Mozambique was richer (29 species) than the South African fauna (24 species). The fauna of Bassas da India was similar to that on the African mainland coast with four additional species. Compared with other areas in the Indo-Pacific, South East Africa has a moderately rich Faviid fauna. Field and laboratory characteristics for each species are described in detail.

Introduction

The hard coral family Faviidae is one of the most important scleractinian coral families both ecologically and in terms of the number of genera and species, particularly in South East Africa, where Faviidae are always among the dominant corals.

The African coral fauna is still very poorly known, with the exception of certain genera, which have received detailed treatment (see Part I, Chapter II). The South East African coral fauna is however of special interest, as the southernmost coral communities on the African continent occur here.

The present chapter describes all species of the family Faviidae, which have so far been found from the subtropical African South-East coast (south of the tropic of Capricorn), as well as those recorded from the Atoll Bassas da India in the Mozambique channel.

Material and Methods

Representative collections were obtained from most reefs in the area. Principal collecting stations were in all three South African reef complexes and on Inhaca Island, off Maputo in southern Mozambique. The material from Mozambique was collected by Dr. P. Boshoff. His collection and publications (Boshoff, 1980; 1981) have been revised in the light of more recent taxonomic information than was available to him. Most other material was collected by the author. The exact localities of the collecting stations are the same as in chapter 2 and outlined there.

The museum collections in which the specimens can be found, are indicated by an abbreviation preceding the index number: SAM is

South African Museum in Cape Town, ORI is Oceanographic Research Institute in Durban, ZMTAU is Zoological Museum of the University of Tel Aviv.

FAMILY FAVIIDAE Gregory, 1900

Not only in southern Africa, but worldwide are the Faviidae one of the most important coral genera, both ecologically and in number of genera and species. Most coral reef areas of the Indo-Pacific are at least to some degree dominated by Faviidae. It is the biggest family in number of genera and the second biggest in number of species, only surpassed by the Acroporidae (Veron et al., 1977). The usual growth form in this family is massive, with only one genus, Echinopora, typically being laminar. Identification clues are offered by corallite size, shape and condition; whether plocoid, cerioid or meandroid. While this generally makes identification easy, intrageneric variability, particularly in Favia, Favites and Goniastera, where intermediate stages occur quite frequently, often cause difficulty in delimiting these genera. Additional important differentiating tools are the mode of budding, whether extra- or intratentacular. These characters are described in detail for each genus.

GENUS FAVIA Oken, 1815

Generic synonymy

Favia Oken, 1815; Edwards & Haime (1857); Matthai (1914), Vaughan (1918); Vaughan & Wells (1943); Alloiteau (1957), Wells (1956); Chevalier (1971, 1972); Veron, Pichon & Wijsman-Best (1977); Sheppard & Sheppard (1991).

Characters

Favia is a very common genus with a world wide distribion. The most commonly encountered growth form is massive and the colonies can reach large sizes. The genus is characterized by the following traits (after Chevalier, 1971):

1) Corallites are generally well separated. However, they sometimes show a tendency to fuse, similar to the genus Favites.
2) Budding is mainly intratentacular, mono- to tristomodeal; however, in certain species (Favia laxa Klunz.) both forms of budding, intra- as well as extratentacular, can be observed.
3) True, multitrabecular pali can be present, madeup of one uniform fan system. Otherwise paliform spines are formed by one simple or compound trabeculum.

FAVIA FAVUS (Forskal, 1775)

(Plate 1a)

Synonymy

Madrepora favus Forskal, 1775.

Favia favus (Forskal); Matthai (1914, 1923); Crossland (1952); Wells (1954); Chevalier (1971); Wijsman-Best (1972, 1974); Scheer & Pillai (1974); Pillai & Scheer (1976); Faure (1977); Veron, Pichon & Wijsman-Best (1977); Wijsman-Best, Faure & Pichon (1980); Scheer & Pillai (1983); Veron (1986); Sheppard (1987); Veron (1988); Sheppard & Sheppard (1991).

Material examined

8 specimens from 2-Mile Reef, Central Reef Complex, RSA (ORI/S2/2-

12-13/13, ORI/S2/2-9-10/10, ORI/S2/2-1-2/6, ORI/S2/2-5-6/20, ZMTAU/V-C-26, ZMTAU/VI-B-4, ZMTAU/IV-F-19, ZMTAU/IV-B-12)

Corallum

From submassive and flat to massive, hemispherical.

Corallites

Round to oval, evenly spaced, intercalicular groove never less than 1.5 mm but up to 4 mm.

Septa

Not clearly arranged in orders, however, often 2 to 3 size classes which do not necessarily represent alternating cycles; larger septa usually meet the columella. Some septa with paliform lobes and well developed dentations of more or less uniform size, fine granulations (finer than in F. speciosa). All septa are evenly exsert.

Costae

Septocostae well developed, large dentations of the same size as on the costae which extend a short way onto the coenosteum.

Columella

Less developed than in most other Favia, trabecular, spongy, incorporating twisted septal teeth.

Coenosteum

Blistered.

Observations

This common Indo-Pacific species is very frequent on all reefs in Maputaland. It is close to Favia speciosa, but generally distinct. It differs in larger corallite size (more than 10 mm, generally up to 15 mm), markedly plocoid growth form and less crowded corallites. Septa are exsert and bear long dentations, similar in

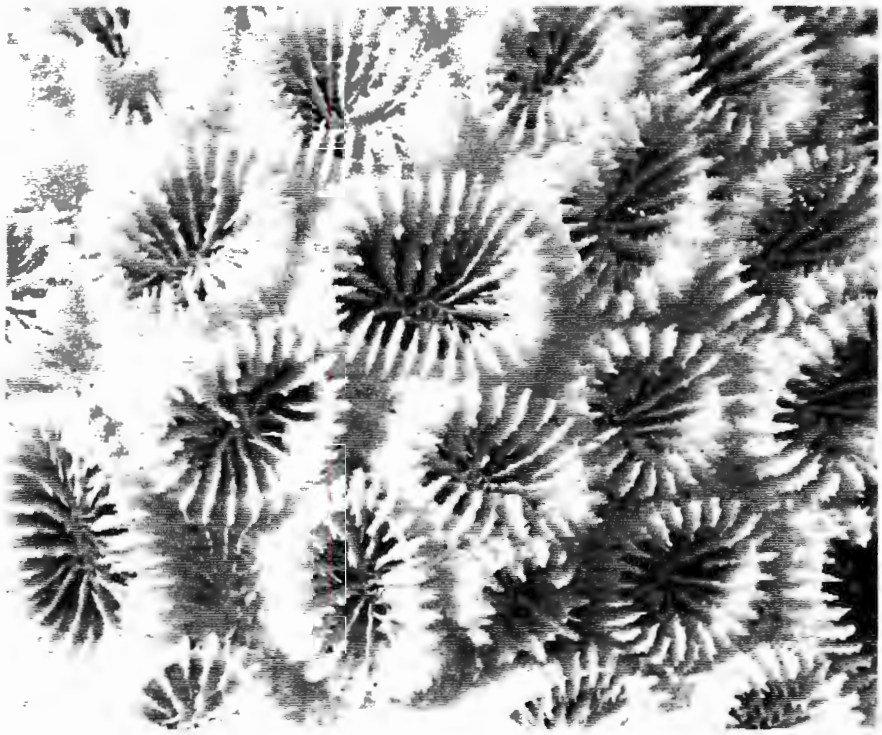


Plate 1a: Favia favus, 2-Mile Reef, South Africa, x2.

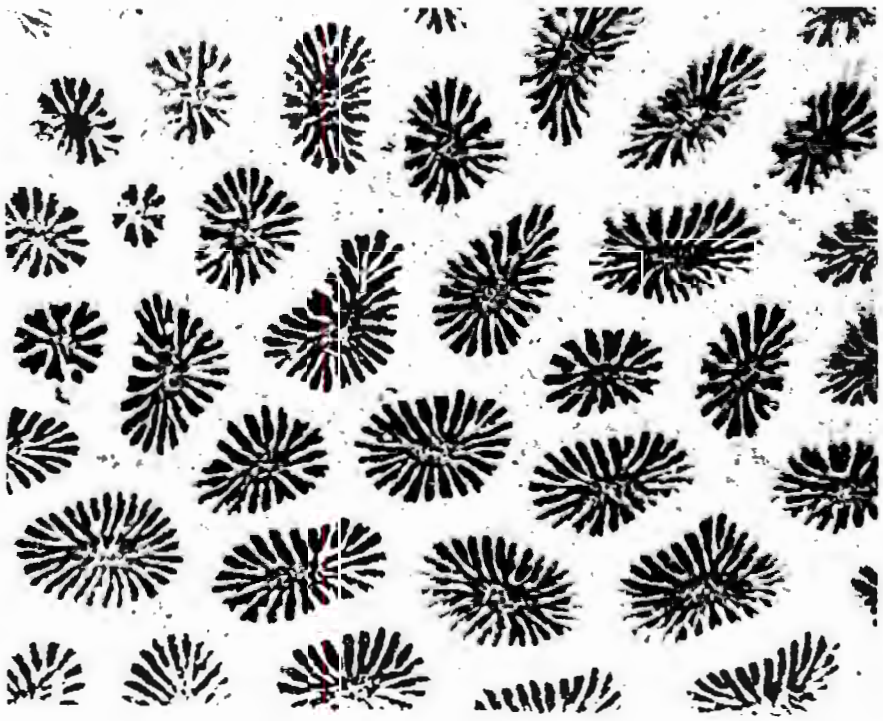


Plate 1b: Favia pallida, 2-Mile Reef, South Africa, x2.

appearance to those in some specimens of Favia speciosa (these differences are most obvious between specimens ORI/S2/2-1-2/6 and ORI/S2/2-6-7/5). Carinae may be found on the exsert septa (ORI/S2/2-12-13/13). The section of the septa over the theca is slightly (ORI/S2/2-2-3/15, ORI/S2/2-1-2/6) to markedly thickened (ORI/S2/2-12-13/13, ORI/S2/2-9-10/10, ORI/S2/2-1-2/6). The columellae are modestly developed in all coralla of the present series, spongy and always incorporating twisted septal teeth. The present series compares well to the variation "robusta" of Chevalier (1971).

FAVIA PALLIDA (Dana, 1846)

(Plate 1b)

Synonymy

Orbicella pallida Dana, 1846.

Favia pallida (Dana); Vaughan (1918); Matthai (1923); Hoffmeister (1925); Yabe & Sugiyama (1935); Wells (1954); Pichon (1964); Chevalier (1971); Rosen (1971); Wijsman-Best (1972, 1974); Pillai & Scheer (1973); Scheer & Pillai (1974, 1976); Faure (1977); Veron, Pichon & Wijsman-Best (1977); Wijsman-Best, Faure & Pichon (1980); Scheer & Pillai (1983); Veron (1986); Sheppard (1987); Veron & Marsh (1988); Veron (1990); Sheppard & Sheppard (1991).

Material examined

5 specimens from 2-Mile Reef, Central Reef Complex, RSA (ORI/S2/2-1-2/10, ORI/S2/2-3-4/7, ORI/S2/2-14-15/12, ZMTAU/IV-B-15, ZMTAU/IV-C-29), 5 specimens from Inhaca Island, Mocambique (ORI/CVIf1(1), ORI/CVIf1(2) and ORI/CVIf1(4) from Baixo 213, ORI/CVIf1(3) and ORI/CVIf2(3) from Pta. Torres).

Corallum

In all specimens massive, hemispherical, plocoid.

Corallites

Round, oval to polygonal where crowded, diameter varies between 5 to 12 mm, exsert to 2 mm, deep calices.

Septa

Mostly in two orders; first order always reach the columella, descend steeply into the calyx, distinct paliform lobes, exsert, thickened over the theca (exept in ORI/CVIf1(2)), dentate, with only very fine granulations; second order: do not always reach the columella, some with paliform lobe.

Costae

Present, differentiated into first and second order costae, of equal size (ORI/CVIf1(2)) or of different size (ORI/CVIf1(3) and (4)), dentate.

Columella

Always present, development varies, usually very dense.

Observations

The three specimens from South Africa form a very homogenous series, which differs from F. favus in corallite size and crowding, the clear development of paliform lobes and different structure of the columella. The septa bear fine spines and are finely granulated. The columella consists of rod-like trabeculae and it does not integrate septal teeth as much as in Favia favus. The South African specimens represent an ecotype with small dentations. They are similar to the variation "amplior" of Chevalier (1971), an ecotype from wave- or current-exposed habitats.

In the Mozambiquan specimens two extreme ecotypes are represented. ORI/CVIf1(2) is hemispherical with thin septa, which are not thickened over the theca and a very compact columella presumably from a sheltered habitat. ORI/CVIf4(3) is also hemispherical but with more crowded calices, thick septa which are thickened over the theca and 2 mm exsert, a loose columella, composed of a few trabeculae and twisted paliform lobes. It is most likely an ecotype of an exposed habitat.

Boshoff (1981) erronously used the name Favia fragum (Esper), an Atlantic species, for one specimen (ORI/CVI1(4)).

FAVIA SPECIOSA (Dana, 1846)

(Plate 2a)

Synonymy

Astrea speciosa Dana, 1846.

Favia speciosa (Dana); Vaughan (1918); Wells (1954); Chevalier (1971); Pillai & Scheer (1976); Faure (1977); Boshoff (1981); Veron & Pichon (1982); Scheer & Pillai (1983); Veron (1986); Sheppard (1987); Sheppard & Sheppard (1991).

Material examined

5 specimens from 2-Mile Reef, Central Reef Complex, RSA (ORI/S2/2-1-2/8, ORI/S2/2-5-6/11, ORI/S2/2-6-7/5, SAM-H-4676 , ZMTAU/V-A-21), 1 specimen from 9-Mile Reef, Central Reef Complex, RSA (SAM-H-4678), 1 specimen from Inhaca Island, Mozambique (ORI/CVIf2(3) from Cabo da Inhaca).

Corallum

Massive, flat to hemispherical, plocoid.

Corallites

Often crowded and polygonal, unequal, spacing 2.5-3.5 mm, deep calices (up to 9 mm), average diameter around 8 mm.

Septa

In number and disposition very similar to F. pallida; thin, regularly exsert, not all reach the columella, fragile teeth on the peripheral part, irregular teeth on the inner part, paliform lobe or spine not always present, generally less conspicuous than in F. pallida.

Costae

In two alternating size classes, extend far onto the coenosteum.

Columella

Spongy, of twisted trabeculae, integrating septal teeth, often not very well developed.

Observations

The differences between F. speciosa and F. pallida are rather ill defined. The corallites of F. speciosa have more crowded, unequal and bigger calices, longer dentations and more obvious paliform lobes in F. speciosa than in F. pallida (Chevalier, 1971; Veron et al., 1977). On South African reefs this species is very common and therefore very well represented in the collection. This observation supports the statement in Veron (1986), that F. speciosa is only common in southern localities, outside the major reef-belt. In the present collection this species is close to F.pallida in calyx size and crowding. However, calices in F. speciosa are more often polygonal. Septa bear longer spines and rougher dentations. As most specimens of these two species were collected on the same reef, and within the same or very similar

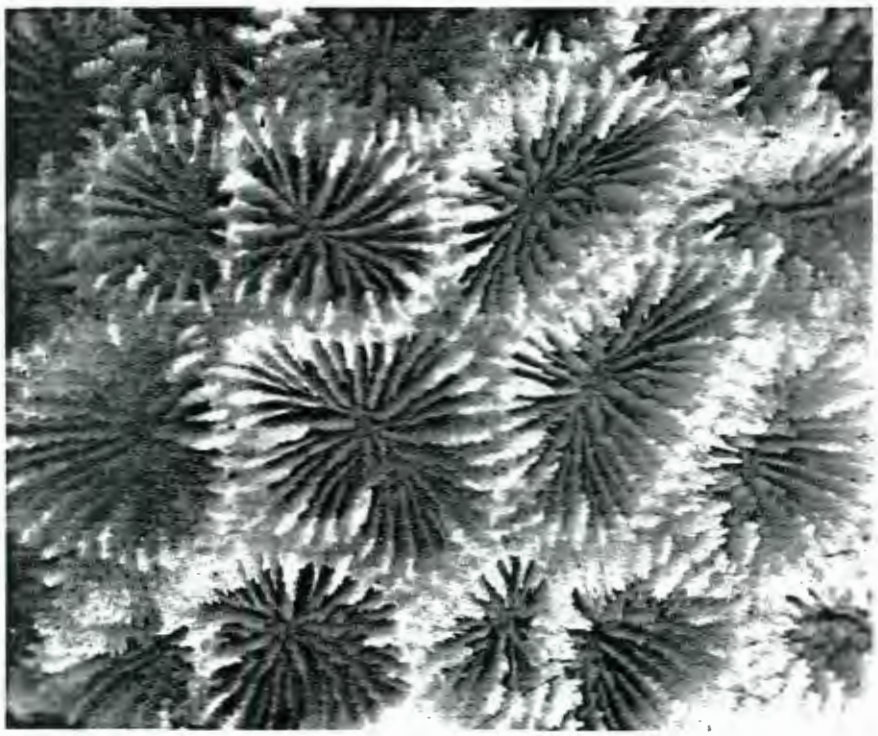


Plate 2a: Favia speciosa, 2-Mile Reef, South Africa, x3.

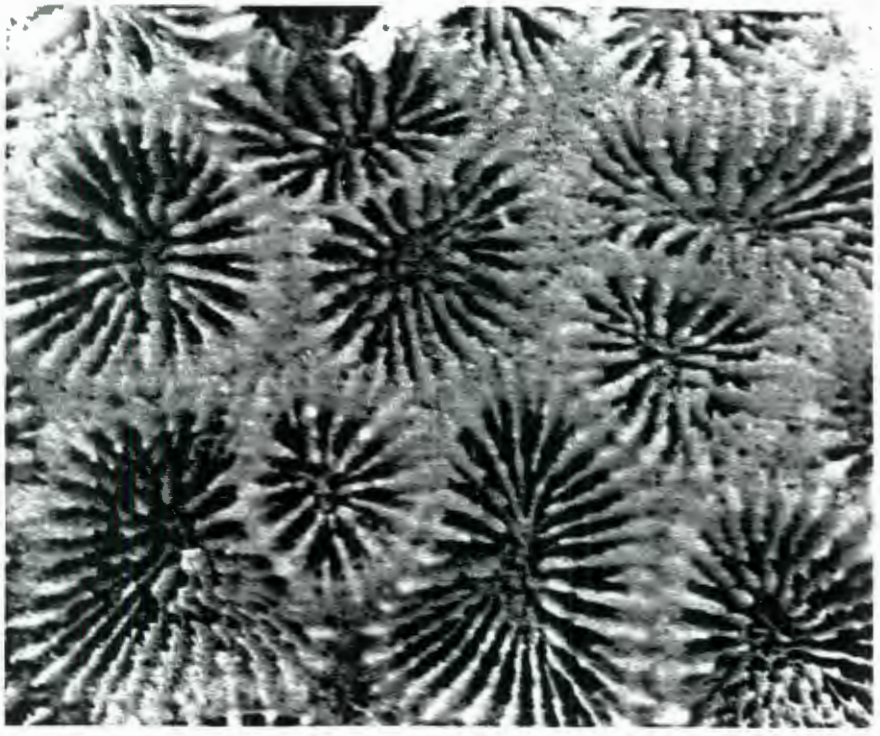


Plate 2b: Favia matthaii, 2-Mile Reef, South Africa, x5.

habitats, the differences in granulation and dentation of the septa are considered to be species-specific and are therefore used to seperate the species.

FAVIA MATTHAII Vaughan, 1918

(Plate 2b)

Synonymy

Favia matthaii Vaughan, 1918; Wijsman-Best (1972, 1974); Veron, Pichon & Wijsman-Best (1977); Veron (1986); Sheppard (1987); Veron & Marsh (1988); Veron (1990).

Favia matthai Vaughan; Sheppard & Sheppard (1991).

Material examined

1 specimen from Two-Mile Reef, Central Reef Complex, RSA (ORI/S2/2-7-8/17).

Corallum

Massive, hemispherical.

Corallites

Round to oval, deformed where crowded, separated by a narrow intercalicular groove, diameter 5-10 mm.

Septa

In three orders; third order abortive, first order twice the length and thickness of second order, distinct crown of large paliform lobes on first order septa, rarely on second order; septa ornamented with spines, which may bear further dentations; septa thickened over the theca; rough granulations on septal sides.

Costae

Septocostae; first and second order of same size, third order appears as intercostal ridge; bearing spines.

Columella

Moderately developed, spongy, consisting of twisted and fused trabeculae.

Observations

This species is apparently rare. It is distinguished by the clearly differentiated three septal cycles and the very distinct crown of paliform lobes on the primary septa, which is better developed than in all other Favia in the collection.

FAVIA LAXA (Klunzinger, 1879)

(Plate 3a)

Synonymy

Orbicella laxa Klunzinger, 1879; Gardiner (1904); von Marenzeller (1907).

Favia laxa (Klunzinger); Matthai (1914); Faure (1977); Veron, Pichon & Wijsman-Best (1977); Boshoff (1981); Scheer & Pillai (1983); Veron (1986); Sheppard (1987); Sheppard & Sheppard (1991).

Material examined

1 specimen from Inhaca Island, Mozambique (ORI/CVIf5(1)).

Corallum

Massive, hemispherical.

Corallites

Plocoid, exsert to 3 mm, round to irregular where crowded, diameter up to 6 mm.

Septa

In two orders; first order septa reach the columella and have a crown of conspicuous paliform lobes, which form a crown around the

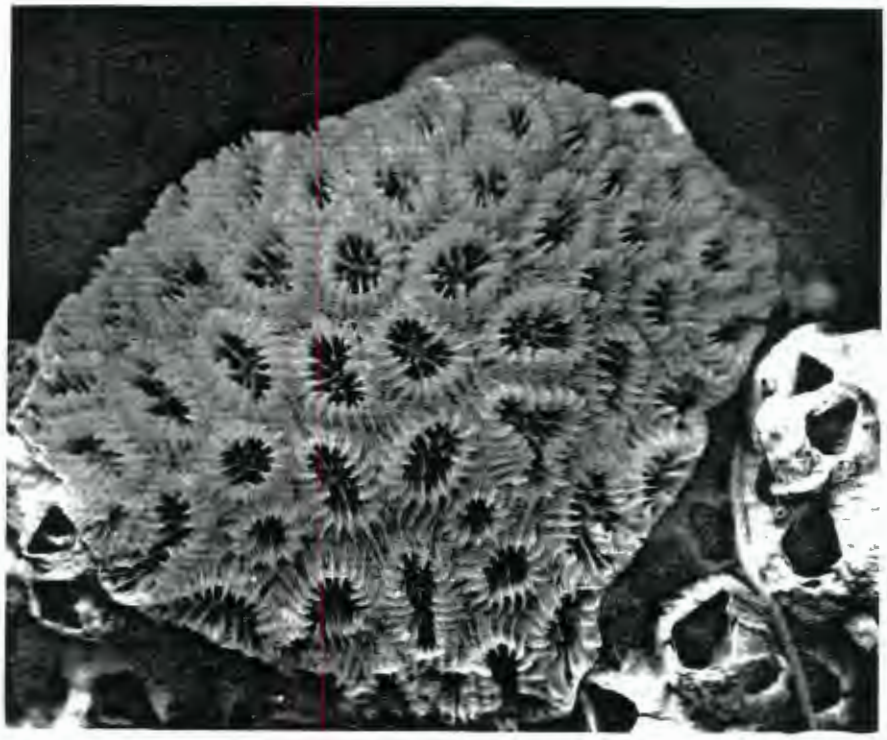


Plate 3a: Favia laxa, Inhaca Island, Mozambique, x2.

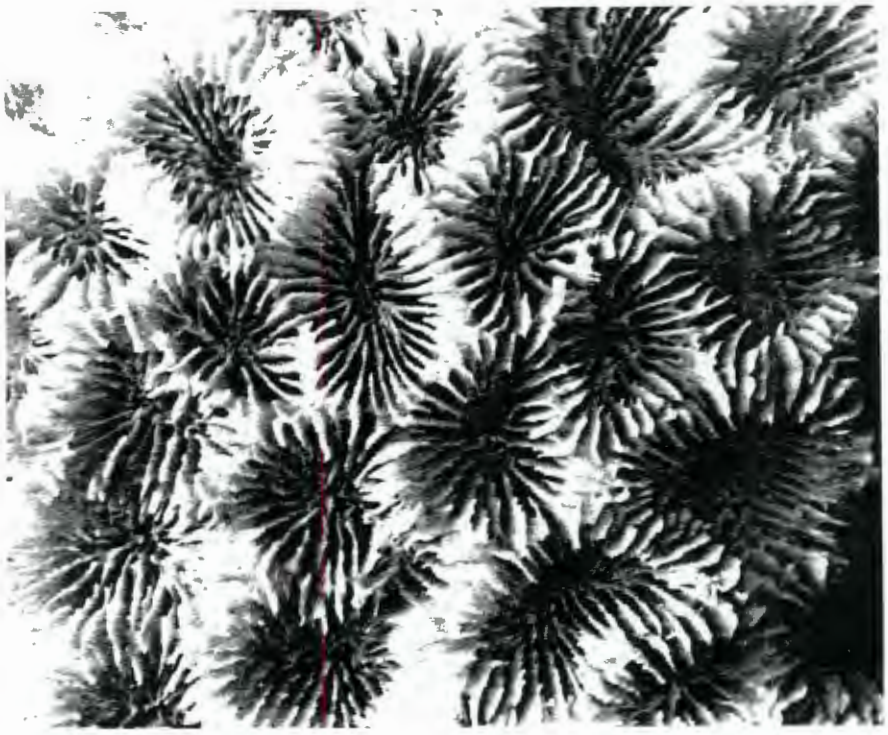


Plate 3b: Favia rotumana, Inhaca Island, Mozambique, x2.5.

columella; septa dentate and with granulated sides, exsert over the thecae; second order septa do not reach the columella and have no paliform lobes.

Costae

Septocostae well developed in two cycles corresponding to the septal cycles; costae of neighbouring corallites do not join.

Columella

Small to well developed, trabecular.

Coenosteum

Smooth with blisters.

Observations

This species is apparently rare. It has also been encountered on South African reefs, but not collected. It differs from the other Favia by its smaller, very regular corallites, only finely dentated septa and regular costae.
This identification requires further verification.

FAVIA ROTUMANA (Gardiner, 1899)

(Plate 3b)

Synonymy

Astrea rotumana Gardiner, 1899.

Favia rotumana (Gardiner); Hoffmeister (1925); Yabe & Sugiyama (1935); Wells (1954); Chevalier (1971); Wijsman-Best (1972, 1974); Scheer & Pillai (1974); Pillai & Scheer (1976); Veron, Pichon & Wijsman-Best (1977); Wijsman-Best, Faure & Pichon (1980); Veron (1986); Sheppard (1987);Veron & Marsh (1988); Sheppard & Sheppard (1991).

Material examined

3 specimens from Nine-Mile Reef, Central Reef Complex, RSA (ORI/

S9/1991-6-6, ORI/S9/1992-1-17, ORI/S9/1991-1-18), 1 specimen from Inhaca Island, Mozambique (ORI/CIIIal(3) from Cabo da Inhaca).

Corallum

Massive, flat to hemispherical.

Corallites

Large, diameter 12-25 mm, crowded, therefore often deformed, budding always intratentacular, moderately to well exsert (3.5 mm on ORI/S9/1992-1-18, up to 12 mm on ORI/S9/1991-6-6).

Septa

In three size classes which do not correspond to the cycles; first order very big, mostly with conspicuous paliform lobe, well exsert, with strong dentations often ornamented by trabecular spines, which in some instances turn into carinae on the exsert part of the septum; second order usually half the size of the first order but with dentations of the same size, paliform lobes mostly present, reach the columella, often exsert to the same extent as first order; third order small, does not reach the columella, but with similar dentations as the first two orders, exsert to a much smaller extent; all septa with large granules on the sides.

Costae

Well developed, mostly equal between all three orders, though in some corallites two orders may be present, with prominent spines, costae of neighbouring calices may or may not fuse.

Columella

Well developed, spongy, set deep inside the calyx.

Coenosteum

With characteristic blisters.

Observations

This species is very characteristic and easily recognized by its large sized calices and the irregular, well exsert and spiny septa.

FAVIA sp.1

(Plate 4a)

Material examined

1 specimen from Inhaca Island, Mozambique (ORI/CVIf2(2) from Baixo 213).

Corallum

Massive, hemispherical, plocoid.

Corallites

Well spaced, round to oval, exsert to 4 mm, diameter up to 20 mm.

Septa

In two to three orders; first order reaches the columella and has paliform lobes on most septa, strongly dentate but much finer than in F. speciosa; exsert over the theca up to 2 mm; second order septa do not reach the columella, no paliform lobes, dentate; third order septa, where present, are only a thin lamella.

Costae

Septocostae well developed, dentate; costae of neighbouring calices do not fuse.

Coenosteum

Smooth with exothecal blisters.

Observations:

This specimen could be an extreme growth form of Favia favus or, at least, is very close to it. It also compares well to the

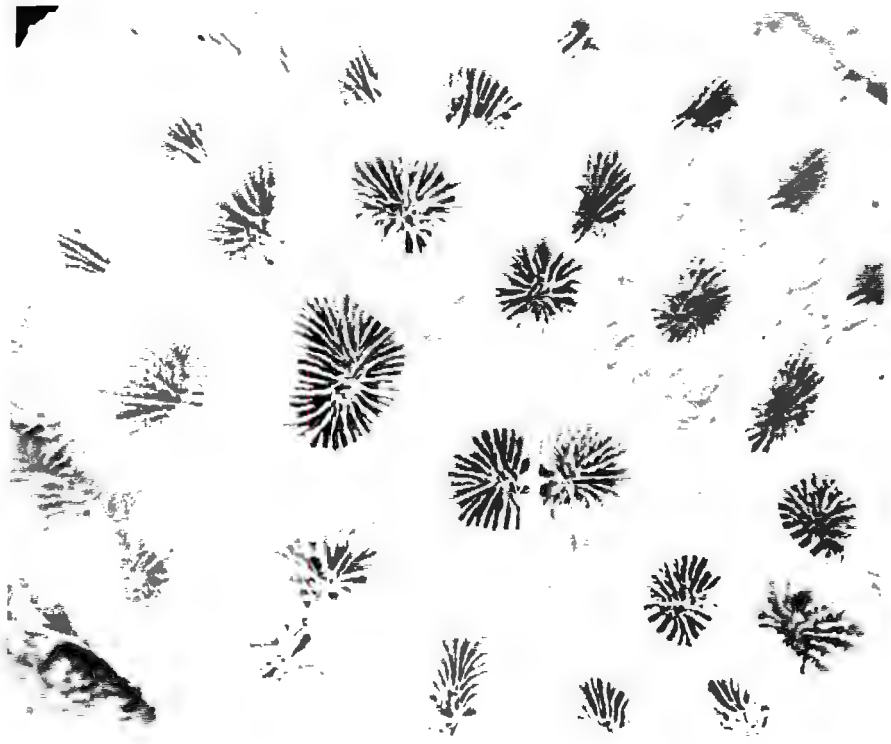


Plate 4a: Favia sp.1, Inhaca Island, Mozambique, x1.5.

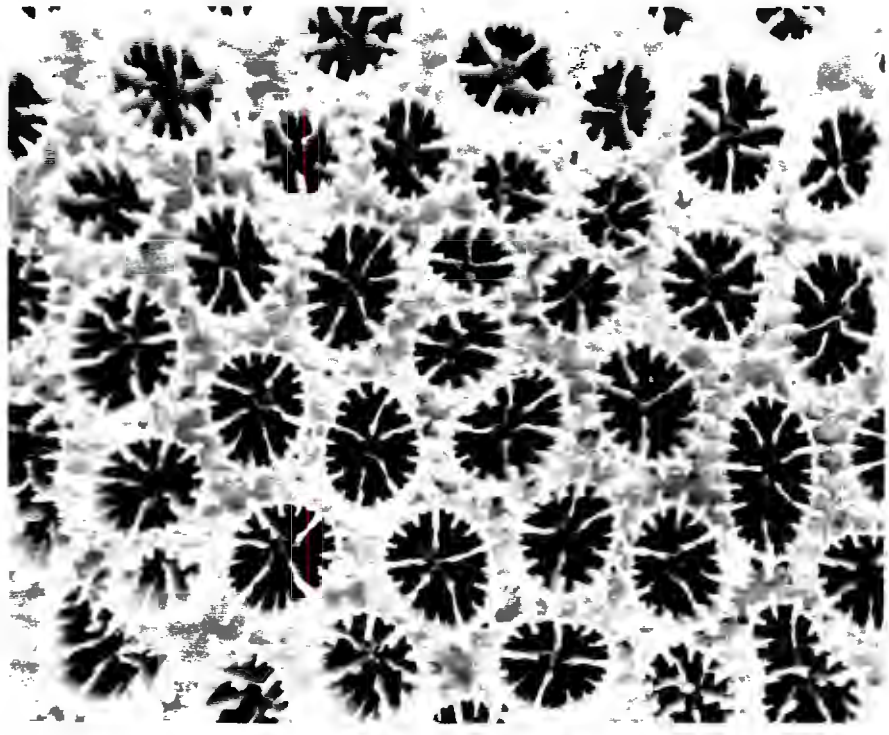


Plate 4b: Favia stelligera, Inhaca Island, Mozambique, x5.

description of Favia sp.1 on page 48 in Veron et al. (1977). While the present specimen also has very large calices and is similar in most other characters, the thecae are less exsert than in the Australian specimens.

FAVIA STELLIGERA (Dana, 1846)

(Plate 4b)

Synonymy

Orbicella stelligera Dana, 1846.

Favia hombroni (Rousseau); Edwards & Haime (1857); Faure (1977).

Favia stelligera (Dana); Vaughan (1918); Hoffmeister (1925); Crossland (1952); Yabe & Sugiyama (1935); Wells (1954); Chevalier (1971); Wijsman-Best (1972, 1974); Scheer & Pillai (1974); Pillai & Scheer (1976, 1983); Veron, Pichon & Wijsman-Best (1977); Wijsman-Best, Faure & Pichon (1980); Veron (1986); Sheppard (1987); Veron & Marsh (1988); Veron (1990); Sheppard & Sheppard (1991).

Material examined:

1 specimen from Inhaca Island, Mozambique (ORI/CVIj1(1)), 2 specimens from Two-Mile Reef, Central Reef Complex, RSA (ORI/S2/1991-2-17, ORI/S2/1991-2-18).

Corallum

Massive, hemispherical.

Corallites

Round to oval, evenly spaced, exsert by 1-2 mm, diameter around 4 mm.

Septa

In 2 orders; in large corallites a third, very reduced third order

cycle is visible; first order septa reach the columella and have well formed paliform lobes, these can be separated from the septa by a series of pores (in ORI/CVIj1(1) not in ORI/S2/1991-2-17 & -18), second order septa only half the size of first order and may lack the paliform lobes; all septa equally exsert above the theca and slightly thickened.

Costae

Only septocostae, these well developed on first order only.

Columella

Inconspicuous to moderately well developed, consisting of twisted trabeculae.

Coenosteum

Smooth with some blisters.

Observations:

The Southern African representatives of this species never exhibit the massive columnar growth form which is typical in many areas of the tropics. All the present specimens are very small. ORI/CVIj1(1), a whole colony, is only 20cm in diameter and no bigger colonies have yet been observed, which is surprising, bearing in mind how huge these colonies can get in the tropics. Boshoff (1981) identified the present specimen as "Leptastrea bottai" (Mn.E.& H.).

GENUS BARABATTOIA Yabe & Sugiyama, 1941

Generic synonymy

Barabattoia Yabe & Sugiyama, 1941; Veron & Pichon (1982); Veron (1986); Sheppard (1987); Veron & Marsh (1988); Veron (1990).

Parastrea Edwards & Haime, 1850.

Bikiniastrea Wells, 1954.

Favia (Oken) Wijsman-Best (1972, 1974); Veron, Pichon & Wijsman-Best (1977); Wijsman-Best, Faure & Pichon (1980); Scheer & Pillai (1983).

This is a somewhat problematic genus, with an unstable taxonomic history. A detailed discussion can be found in Veron et al. (1977) and Veron & Pichon (1982).

The growth form is massive with well exsert corallites. Pali are absent or only weakly developed. Budding is mono- or distomodeal, also intercalicular.

BARABATTOIA AMICORUM (Edwards & Haime, 1850)

(Plate 5a)

Synonymy

Parastrea amicorum Edwards & Haime, 1850.

Favia amicorum (Edwards & Haime); Wijsman-Best (1972, 1974); Veron, Pichon & Wijsman Best (1977); Wijsman-Best, Faure & Pichon (1980); Scheer & Pillai (1983).

Barabattoia amicorum (Edwards & Haime); Veron & Pichon (1982); Veron (1986); Sheppard (1987); Veron & Marsh (1988); Veron (1990).

Material examined

1 specimen from Inhaca Island, Mozambique (ORI/CIIIal(1) from Pta. Torres).

Corallum

Ramose.

Corallites

Oval, exsert by 5-10 mm, diameter up to 15 mm, no anastomoses,

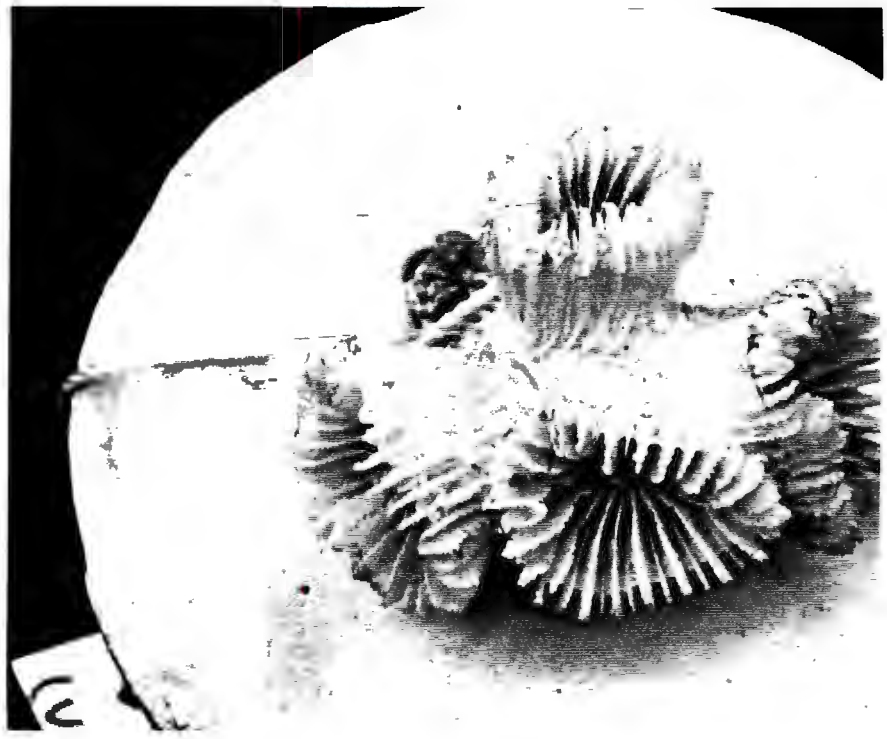


Plate 5a: Barabattoia amicorum, Inhaca Island, Mozambique, x2.5.

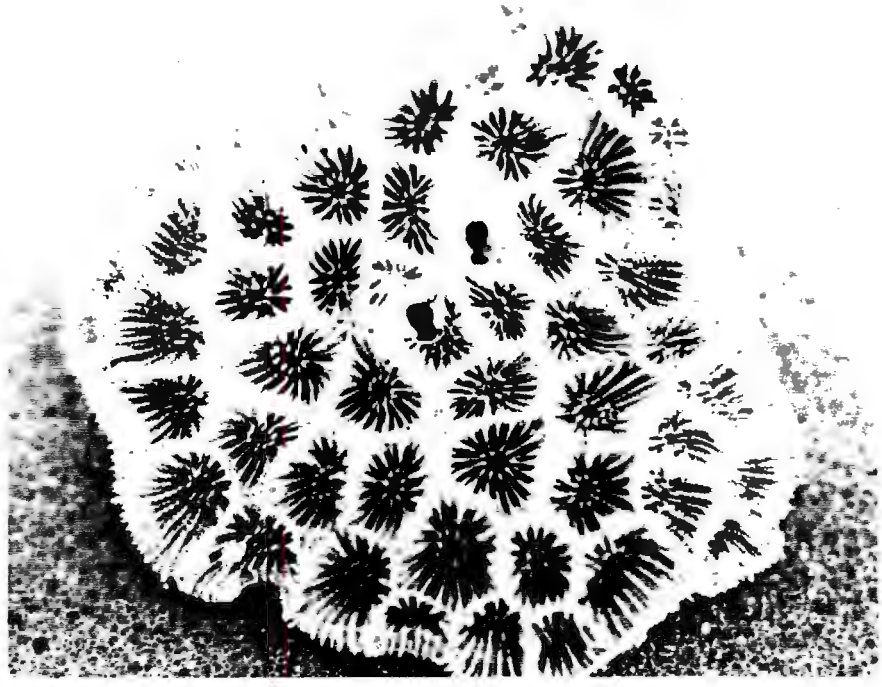


Plate 5b: Favites pentagona, 2-Mile Reef, South Africa, x2.5.

intratentacular budding (monostomodeal) in process.

Septa

In three orders, regularly dentate; well developed paliform lobes on first and second order, missing on third order septa; very distinctive dentations and granulations in form of ridges on the septal sides.

Costae

Well developed, in alternating orders; third order costae abortive; distinctively dentate.

Columella

Well developed, trabecular.

Observations:

Only one small specimen is present in the collection, which, however, very clearly exhibits the characteristica of Barabattoia. According to Veron et al. (1977) and Veron & Pichon (1982) this is an ill-defined genus, which may also include Bikiniastrea Wells, 1954. It has not yet been recorded from the western Indian Ocean and further material would be needed to confirm its presence beyond any doubt. Boshoff (1981) erronously identified this specimen as Caulastrea tumida Matthai.

GENUS FAVITES Link, 1807

Generic synonymy

Favites Link, 1807; Vaughan (1907); Vaughan & Wells (1943); Wells (1956); Chevalier (1971); Veron, Pichon & Wijsman Best (1977).

Characteristics

The main difference between Favites and the genus Favia is the absence of a distinct intercalicinal spacing in Favites, e.g. a

truly cerioid calyx arrangement. In certain species however, (F. flexuosa, F. complanata, F. halicora) there is a progression towards a subcerioid situation.

Favites is also close to Goniastrea as in some instances multitrabecular paliform lobes (i.e. true pali), a characteristic of Goniastrea, can be observed (Chevalier, 1971).

FAVITES PENTAGONA (Esper, 1794)

(Plate 5b)

Synonymy

Madrepora pentagona Esper, 1794.

Favites pentagona (Esper) Yabe & Sugiyama (1935); Crossland (1948); Chevalier (1971); Wijsman-Best (1972); Veron, Pichon & Wijsman-Best (1977); Wijsman-Best, Faure & Pichon (1980); Scheer & Pillai (1983); Veron (1986); Sheppard (1987); Veron & Marsh (1988); Veron (1990); Sheppard & Sheppard (1991).

Material examined

4 specimens from Two-Mile Reef, Central Reef Complex, RSA (SAM-H-4657 & -76, ORI/S2/2-7-8/20, ORI/S2/2-14-15/13), 1 specimen from Nine-Mile Reef, Central Reef Complex, RSA (ORI/S9/1991-2-19); 5 specimens from Inhaca Island, Mozambique (ORI/CVIg4(1) and ORI/CVIg5(2) from Pta. Torres, ORI/CVIg4(2) and ORI/CVIg4(4) from Isla dos Portugueses, ORI/CVIg5(3) from Saco da Inhaca); 1 specimen from Umdloti, Natal coast (ORI/CVIg5(1)).

Corallum

Flat incrusting to submassive and hillocky; cerioid.

Corallites

From polygonal or hexagonal and crowded, to round and not crowded;

in most cases very unequal; diameter 6-10 mm, mostly around 7 mm; budding mostly extratentacular.

Septa

Two to three orders, thin. First order always reaches the columella; not all second order septa reach the columella; third order reduced or abortive. Small, regular dentations, distal edges of septa with numerous small dentations; well developed paliform lobes forming a crown around the coumella; often a trabecular linkage between the the paliform lobe and the septum; septal sides granulated.

Columella

Spongy, of twisted and fused trabeculae.

Theca

Thick.

Observations

The four specimens show a wide variety in growth form, which can most likely be attributed to different environmental conditions. SAM-H-4676 is the most heavily calcified specimen with thick walls, very exsert septa which are markedly thickened over the thecae and strong, spiny dentations. This specimen was collected at an exposed site on Two Mile Reef at 12m depth. The other extreme in the present series is represented by ORI/S9/1991-2-19 a small colony with thin walls, only slightly exsert septa, which are not, or only very slightly, thickened over the thecae and have small, very regular dentations. This specimen shows some resemblance to Goniastrea retiformis. It was collected at 20m depth in a sheltered locality. The other specimens are

intermediate between these two extremes in growth form. Extratentacular budding is evident in all specimens.

FAVITES PERESI (Faure & Pichon, 1978)

(Plate 6a)

Synonymy

Favites peresi Faure & Pichon, 1978.

Favites peresi (Faure & Pichon); Scheer & Pillai (1983); Sheppard (1987); Sheppard & Sheppard (1991).

Material examined

1 specimen from Two Mile Reef, Central Reef Complex, RSA (ORI/S2/1991-9-57), 1 specimen from Nine Mile Reef, Central Reef Complex, RSA (ORI/S9/FFs6), 1 specimen from the Northern Reef Complex, RSA (ORI/KB/1991-9-55); 4 specimens from Inhaca Island, Mozambique (ORI/CVIg3(1) and ORI/CVIg3(3) from Pta. Torres, ORI/CVIg2(2) and ORI/CVIg3(2) from Cabo Inhaca).

Corallum

Massive, hemispherical, cerioid.

Corallites

Large (9-15 mm in the longest axis), polygonal, crowded, deep (around 5 mm), with very acute walls.

Septa

In three orders, in some calyces an abortive fourth order; septa of first and second order bear a distinctive paliform tooth; septa with strong ornamented dentations, unitrabecular spines tend to fuse towards the calyx centre and form multitrabecular lobes; septal sides are granulated.

Columella

Well developed, spongy, consisting of twisted trabeculae, which are fused to the inner edge of the septa.

Thecae

Thick, vesicular endotheca of up to one half of the calyx radius, very conspicuous.

Observations

The quite unique formation of paliform teeth on the septa of the first and second order, together with the very acute walls coupled with the thick endotheca make this species easy to identify. Septa bear strong, vertical dentations, monotrabecular at the distal (close to the theca) part, pluritrabecular on the proximal part. A deep groove seperates the last tooth from the paliform lobe. The septa run only as a low ridge along the wall. In large hemispherical coralla the wall is only acute in the lower part of the corallum, while on the convex upper portion the wall does not protude above the inflated, wide part of the endotheca. This growth form is however the exeption.

F. peresi is common on the reefs in South Africa and Mozambique. The present specimens compare very well to the description of "ecomorphe alpha" in Faure & Pichon (1978) from exposed reef slopes. The environmental conditions on the South african reefs are comparable to those on exposed tropical reef slopes.

Boshoff (1981) identified his specimens from Mozambique as F. spectabilis (Verrill).

Plate 6a: Favites peresi, 4-Mile Reef, South Africa, x1.5.

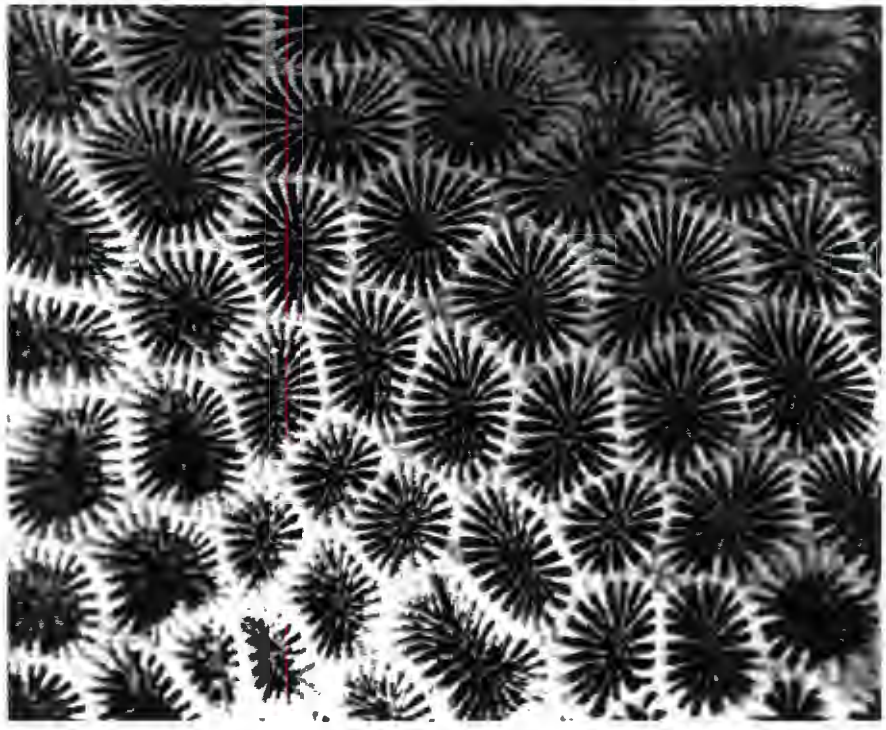


Plate 6b: Favites complanata, 2-Mile Reef, South Africa, x1.5.

FAVITES COMPLANATA (Ehrenberg, 1834)

(Plate 6b)

Synonymy

Favia complanata Ehrenberg, 1834; Matthai (1914).

Favites complanata (Ehrenberg); Chevalier (1971); Veron, Pichon & Wijsman-Best (1977); Wijsman-Best, Faure & Pichon (1980); Scheer & Pillai (1983); Sheppard (1987); Veron & Marsh (1988); Sheppard & Sheppard (1991).

Material examined

2 specimens from Jesser Point, Sodwana Bay, Central Reef Complex, RSA (ORI/S1/FFS2, ORI/S1/Ffs3), 1 specimen from Two-Mile Reef, Central Reef Complex, RSA (ORI/S2/1991-7-29), 1 specimen from Bassas da India, Lagoon (ORI/BdI/1991-8-56), 1 specimen from Inhaca Island, Mozambique (ORI/CVIg1(2) from Pta. Torres).

Corallum

Flat incrusting to massive hemispherical (in the intertidal as well as the subtidal).

Corallites

Crowded, polygonal, however rounder in appearance than in F. abdita or F.flexuosa; diameter 5-14 mm, mostly around 11 mm, cerioid to subcerioid.

Septa

In two orders, they can be of the same size or the second order can be of smaller size or reduced; then only the first order reaches the columella (S1/Ffs2), large dentations, wider spaced than in F. abdita; dentations are ornamented; no fusion of teeth; large teeth also on the exsert section of septum; no development of paliform lobes; granulated septal sides.

Columella

Spongy, trabeculae fused by horizontal plates.

Observations

This species is common on the reefs and in the intertidal in northern Natal, where it forms encrusting to massive, hemispherical colonies. Calyx sizes, calcification, septal dentation and the degree to which septa are exsert are remarkably uniform in all specimens. This species can be separated from F. abdita by its size, the distance between the septal dentations, and the presence of paliform lobes.

FAVITES ABDITA (Ellis & Solander, 1786)

(Plates 7a&b)

Synonymy

Madrepora abdita Ellis & Solander, 1786.

Favites abdita (Ellis & Solander); Vaughan (1918); Yabe & Sugiyama (1935); Crossland (1948, 1952); Wells (1954); Chevalier (1971); Rosen (1971); Wijsman-Best (1972, 1976); Pillai & Scheer (1973, 1974, 1976); Veron, Pichon & Wijsman-Best (1977); Faure (1977); Scheer & Pillai (1983); Sheppard (1987); Veron & Marsh (1988); Veron (1990); Sheppard & Sheppard (1991).

Astraea virens Dana, 1846.

Material examined

1 specimen from Jesser Point, Sodwana Bay, Central Reef Complex, RSA (ORI/S1/FFS4), 1 specimen from 2-Mile Reef (SAM-H-4644, 1 specimen from Bassas da India, Lagoon (ORI/BdI/1991-8-55), 1 specimen from Inhaca Island, Mozambique (ORI/CVIg2(3) from Pta. Torres), 1 specimen from Port St. John, Transkei (ORI/CVIg2(1)).

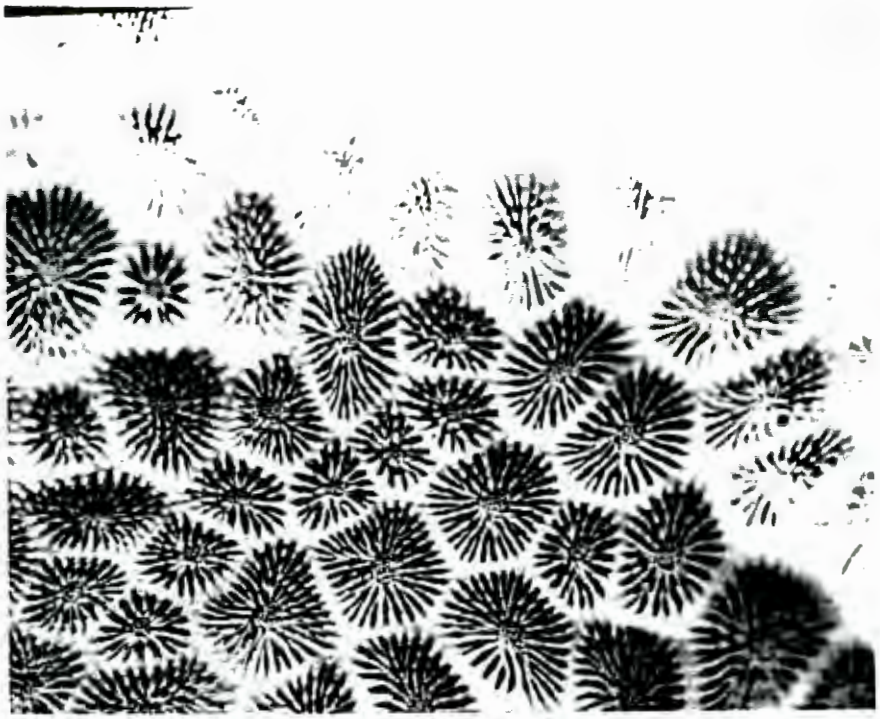


Plate 7a: Favites abdita, Inhaca Island, Mozambique, x1.5.

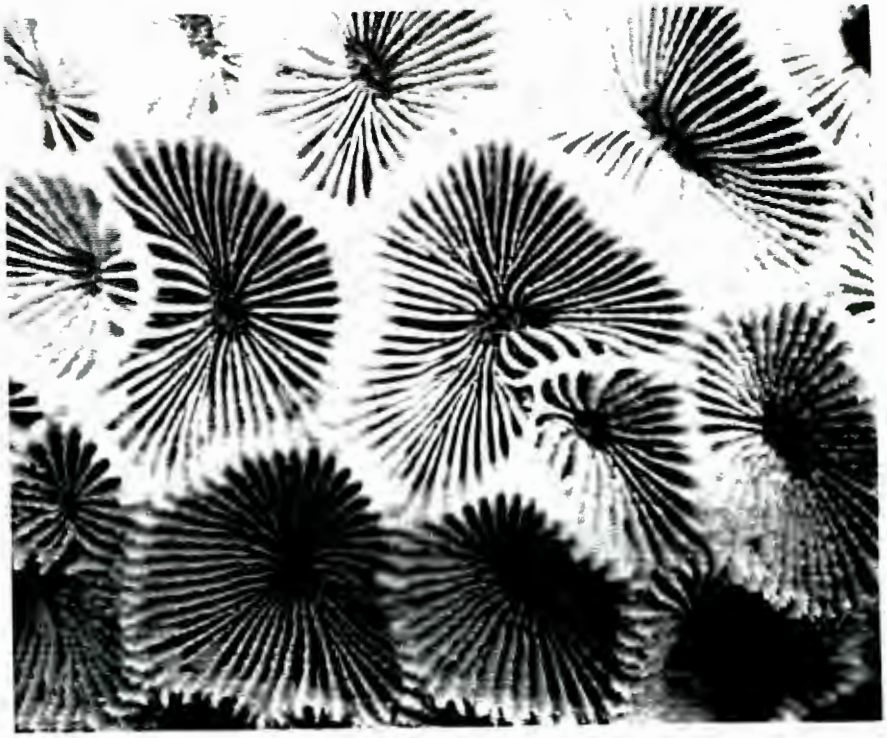


Plate 7b: Favites abdita var. virens, 4-Mile Reef, South Africa, x2.5.

Corallum

Flat incrusting in intertidal specimens, massive hemispherical in subtidal specimens.

Corallites

Polygonal, crowded, diameter 12-18 mm.

Septa

In three to four different size classes which correspond to their orders; first and second cycle meet the columella; conspicuous dentations on all septa which are very uniform in spacing and size, rarely fusion of adjacent teeth, no formation of either paliform lobes or true pali .

Columella

Spongy, consisting of rod-like trabeculae.

Thecae

Thin; only thick on hillocky specimens (BdI/1991-8-55).

Observations

F. abdita is common and occurs over a wide range of habitats from the intertidal to the deep subtidal. A fragment of one colony, collected in a tidal pool, was encrusting, showing the typically large corallites of the species. Septal dentation was strong, related to the fact that it came from an exposed environment. The columellae varied in their development from consisting of only a few trabeculae to well developed and spongy.

The subtidal specimens from the Northern Reef Complex show small, very regular dentations. ORI/BdI/1991-8-55 is a hillocky specimen with small corallites. ORI/CVIg2(3) from Pta. Torres is close to the type specimen of Favites virens possessing thin septa and walls, and having septa that are clearly arranged in 2-3 size

classes, which do not always correspond to orders. It clearly falls within the variability of the F. abdita specimens. I therefore agree with Veron et al. (1977), who consider F. virens a synonym of F.abdita.

Boshoff (1981) identified his specimens from Mozambique as F. halicora (Ehrbg.).

FAVITES FLEXUOSA (Dana, 1846)

(Plate 8a)

Synonymy

Astraea flexuosa Dana, 1846.

Favites flexuosa (Dana); Chevalier (1971); Pillai & Scheer (1976); Veron, Pichon & Wijsman-Best (1977); Wijsman-Best, Faure & Pichon (1980); Scheer & Pillai (1983); Veron (1986); Sheppard (1987); Veron & Marsh (1988); Sheppard & Sheppard (1991).

Material examined

2 specimen from Two-Mile Reef, Central Reef Complex, RSA (ORI/S2/2-7-8/14, ORI/S2/2-6-7/8); 2 specimens from Inhaca Island, Mozambique (ORI/CVIg1(3) from Pta. Torres, ORI/CVIg1(4) from Pta. Rasa); 3 specimens from Bassas da India, lagoon (ORI/BdI/1991-8-57, ORI/BdI/1991-8-58, ORI/BdI/1991-8-59).

Corallum

Submassive, flat.

Corallites

Cerioid with fully fused corallites to subcerioid with intercalicular groove, diameter 10-20 mm.

Septa

In four size classes; all septa equally exsert, rounded over the theca and continue as costae; average number of septa 40; on the distal (outer) part, strong, monotrabecular "astreoid" teeth, which fuse on the proximal part to form pluritrabecular, "mussoid" teeth (Chevalier, 1971); the mussoid teeth may take the appearance of paliform lobes.

Columella

Weak development, consisting of twisted septal teeth and trabeculae.

Thecae

Thin to missing, or made up of trabecular apophyses.

Observations

The specimens form a very homogeneous series. They all have large corallites but can easily be separated from F. abdita by the larger dentations and the wider spacing of the dentations in F. flexuosa. All three specimens from South Africa resemble the variation "magnistellata" of Chevalier (1971).

The presence of mussoid teeth is clearly visible in most specimens. ORI/CVIg1(3) from Inhaca Island differs substantially from the rest of the series by its smaller calyx size (up to 10 mm), very smooth septa and frequent fusion of septa. It was identified as F. flexuosa due to the differentiation of the dentations into monotrabecular and pluritrabecular teeth. However, there remains some doubt as to its true identity.

Boshoff (1981) identified his specimens from Mozambique as F. abdita (Ell. & Sol.).

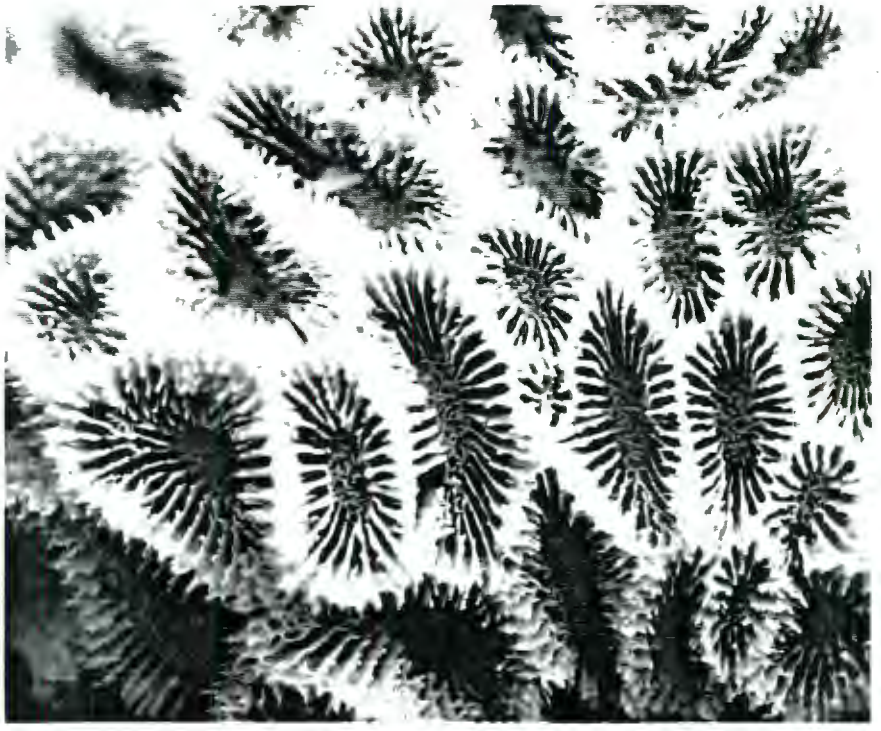


Plate 8a: Favites flexuosa, Bassas da India, x1.5.

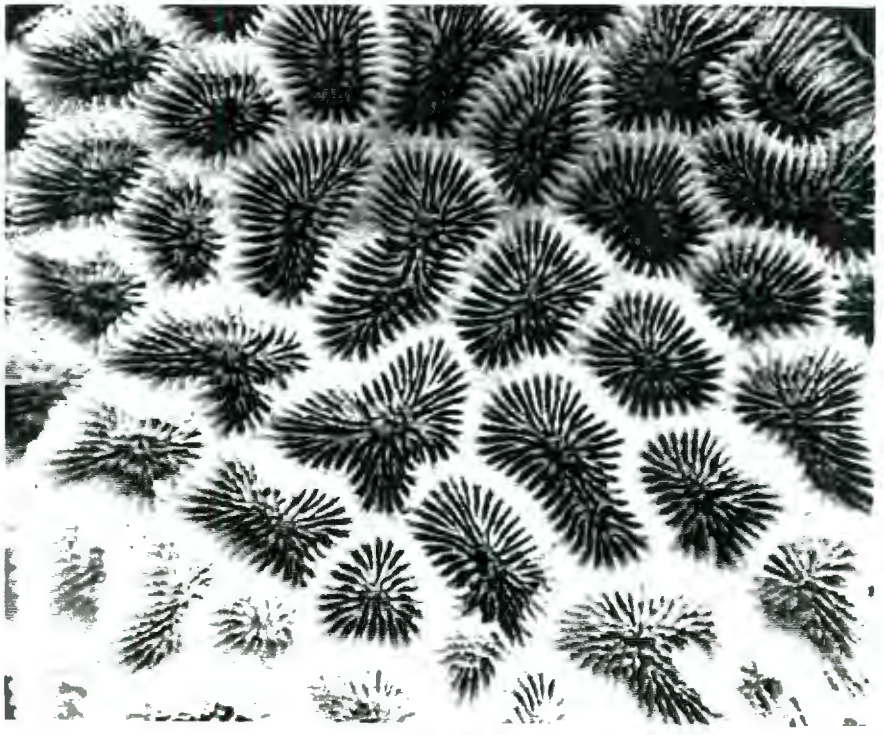


Plate 8b: Favites halicora, Jesser Point, South Africa, x3.5.

FAVITES HALICORA (Ehrenberg, 1834)

(Plate 8b)

Synonymy

Astraea halicora Ehrenberg, 1834.

Goniastrea halicora (Ehrenberg); Klunzinger (1879).

Favia halicora (Ehrenberg); Gardiner (1904); Matthai (1914).

Favites halicora (Ehrenberg); Vaughan (1918); Hoffmeister (1925); Crossland (1948, 1952); Chevalier (1971); Rosen (1971); Scheer & Pillai (1974); Pillai & Scheer (1976); Veron, Pichon & Wijsman-Best (1977); Boshoff (1981); Scheer & Pillai (1983); Veron (1986); Sheppard (1987); Veron & Marsh (1988); Sheppard & Sheppard (1991).

Material examined

1 specimen from Jesser Point, Sodwana Bay, Central Reef Complex, RSA (ORI/S1/Ffs3), 1 specimen from 2 Mile Reef, Central Reef Complex, RSA (ORI/S2/1991-6-8); 1 specimen from Durban, RSA (ORI/CVIf4(1)); 1 specimen from Inhaca Island, Mozambique (ORI/CVIg1(5) from Pta. Torres).

Corallum

Massive, flat.

Corallites

Cerioid, polygonal, without the sharp angles as in F. abdita, diameter 8-14 mm, mostly around 10 mm.

Septa

In two or three cycles, first two cycles of the same size, third cycle, if present, strongly reduced in size; septa descend very abruptly into the calyx, dentations either irregular on the distal edge or very regular throughout on all septa; often a distinct crown of paliform lobes on most corallites made up by 1 to 3 fused

dentations, fusion varies from completely to not at all; if present, dentations continue over the paliform lobe; septal sides granulated.

Columella

Spongy, consisting of rod-like trabeculae.

Thecae

Relatively thick.

Observations

This species is distinct and easy to identify by the thick walls and the well developed paliform lobes. Calices are shallow in intertidal specimens from Northern Natal and Mozambique, only the specimen from Durban has deep calices. Otherwise the 4 specimens form a very homogeneous series.

GENUS GONIASTREA Milne Edwards & Haime, 1848

Generic synonymy

Goniastrea Edwards & Haime, 1848.

Characters

Colonies are ceroid to submeandroid. Budding is mono- to tristomodeal. Goniastrea is close to Favites, but differs by the presence of true pali and a finer ornamentation of the septa.

GONIASTREA PECTINATA (Ehrenberg, 1834)

(Plate 9a)

Synonymy

Astraea pectinata Ehrenberg, 1834.

Goniastrea pectinata (Ehrenberg); Klunzinger (1879); Gardiner (1904); von Marenzeller (1907); Matthai (1914); Vaughan (1918);

Hoffmeister (1925); Yabe & Sugiyama (1935); Crossland (1952); Pichon (1964); Chevalier (1971); Rosen (1971); Wijsman-Best (1972-1976); Scheer & Pillai (1974); Pillai & Scheer (1974, 1976); Faure (1977); Veron, Pichon & Wijsman-Best (1977); Scheer & Pillai (1983); Veron (1986); Sheppard (1987); Veron & Marsh (1988); Sheppard & Sheppard (1991).

Goniastrea columella Crossland, 1948.

Material examined

1 specimen from Two-Mile Reef, Central Reef Complex, RSA (ORI/S2/2-13-14/18).

Corallum

Submassive, flat.

Corallites

Crowded, mono- to polycentric, forming only short series of a maximum of 6 centres; average calyx size or valley width around 5 mm.

Septa

In two orders, often very irregular size differences; septa of different orders often fuse; first order with well developed, usually rounded paliform lobes; septa with fine, regular dentations, sides finely granulated.

Columella

Well developed, spongy, in polycentric calices with trabecular linkage which is fused to the septa and takes the form of a vertical plate.

Observations

The only specimen in the collections shows all stages from a monocentric to a submeandroid condition. Valleys are mostly bi- to

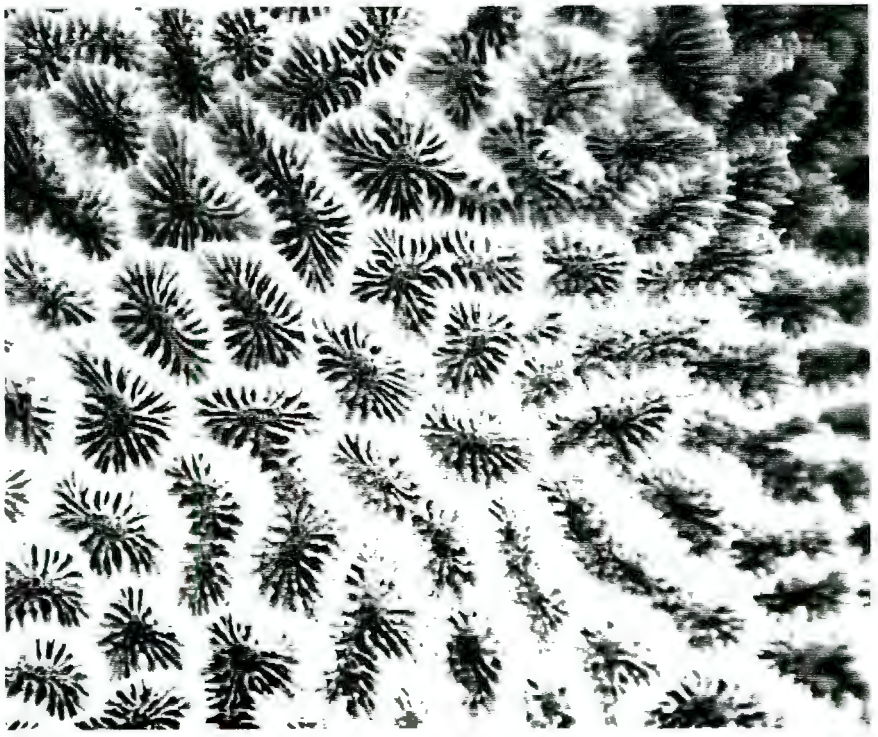


Plate 9a: Goniastrea pectinata, 2-Mile Reef, South Africa, x2.5.

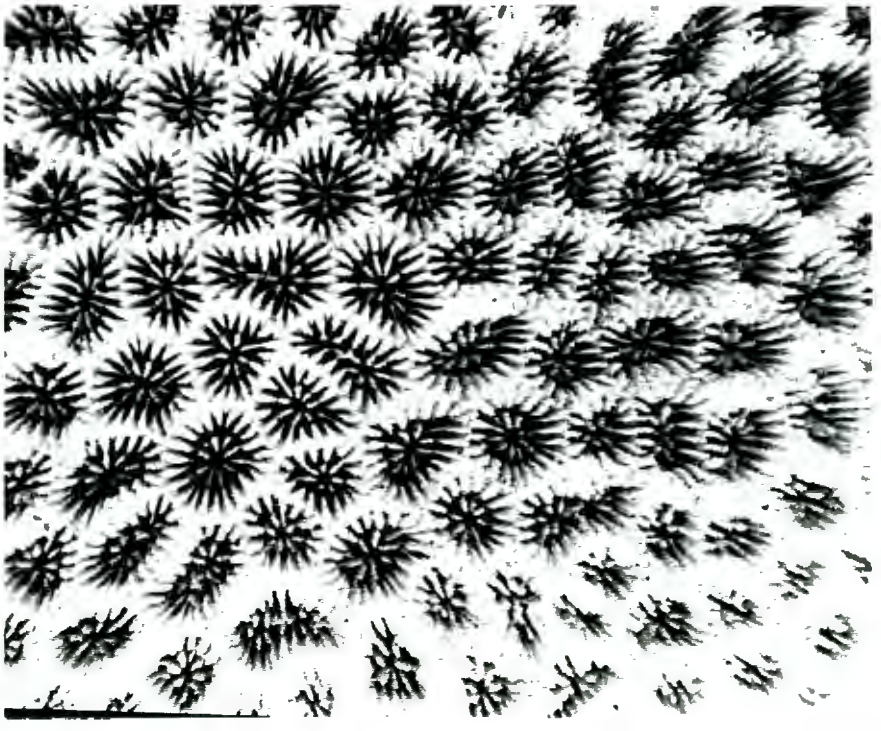


Plate 9b: Goniastrea retiformis, Bassas da India, x4.

tricentric with a maximum of six centres in a few series. The present specimen seems to be an ecomorph from exposed habitats as it tends to have short series rather than long meanders.

Boshoff's (1981, p.30) Goniastrea laxa Quelch is Coeloseris meyeri Vaughan, an agariciid.

GONIASTREA RETIFORMIS (Lamarck, 1816)

(Plate 9b)

Synonymy

Astraea retiformis Lamarck, 1816.

Goniastrea retiformis (Lamarck); Edwards & Haime (1846, 1857); Ortmann (1888); Klunzinger (1879); von Marenzeller (1907); Matthai (1914); Vaughan (1918); Hoffmeister (1925); Yabe & Sugiyama (1935); Crossland (1952); Pichon (1964); Chevalier (1971); Wijsman-Best (1972, 1976); Scheer & Pillai (1974); Pillai & Scheer (1976); Faure (1977); Veron, Pichon & Wijsman-Best (1977); Wijsman-Best, Faure & Pichon (1980); Scheer & Pillai (1983); Veron (1986); Sheppard (1987); Sheppard & Sheppard (1991).

Material examined

2 specimens from Two Mile Reef, Central Reef Complex, RSA (ORI/S2/2-2-3/18, ORI/S2/1991-11-16), 1 specimen from Bassas da India, Lagoon (ORI/BdI/1991-8-37).

Corallum

Typically massive and spherical or flat incrusting.

Corallites

Cerioid, crowded, polygonal (penta- to hexagonal) resulting in a "honeycomb" pattern, always monocentric, diameter 4-7 mm.

Septa

Two to three orders distinguishable, third order often abortive, first and second order usually different in size; first order reaches the columella and forms large paliform lobes, second order does not always reach the columella and paliform lobes are only irregularly formed; septa often joined to the columella; not continuous over the theca; all septa with fine, regular dentations; septal sides finely granulated.

Columella

Spongy, may consist of only a few trabeculae (as in S2/2-2-3/18) or may be well developed.

Thecae

Thin.

Observations

Neither of the two South African specimens show the typical spherical growth form, which is very apparent in the specimen from Bassas da India. ORI/S2/2-2-3/18 is massive but hillocky, while ORI/S2/1991-11-16 is a flat incrusting colony. The corallites in both these specimens are monocentric and polygonal and show the typical honeycomb pattern. In both specimens at least two orders of septa can be discerned in every corallite, the third order being abortive in many. ORI/S2/2-2-3/18 has a thinner and more acute theca with septa not exsert, while ORI/S2/1991-11-16 has exsert septa with strong dentations, which are not continuous over the thecae. In appearance this specimen comes close to G. edwardsi. ORI/S2/2-2-3/18 compares well to the variation "bournoni" in Chevalier (1971), while S2/1991-11-16 seems to be a typical variation "parvistellata" (Chevalier, 1971).

GONIASTREA cf. EDWARDSI Chevalier, 1971

(Plate 10a)

Synonymy

Goniastrea edwardsi Chevalier, 1971; Wijsman-Best (1976); Veron, Pichon & Wijsman-Best (1977); Veron (1986); Sheppard (1987); Sheppard & Sheppard (1991).

Material examined

1 specimen from Two-Mile Reef, Central Reef Complex, RSA (S2/2-10-11/20).

Corallum

Submassive, flat.

Corallites

Crowded, polygonal, though less angular than in G. retiformis, always monocentric, diameter 4-6 mm.

Septa

In three orders, third order abortive and not visible in every corallite; second order usually only 1/2R; first and second order exsert and continuous over the theca, septa of adjacent corallites may fuse or be sepaerated by a narrow groove; regular dentations of the same size on first and second order septa as well as on the palis; palis only well developed on first order septa; septal sides granulated.

Columella

Spongy.

Thecae

Well calcified, thick, diameter 1mm, thicker than in G.retiformis.

Observations

In appearance this species is very similar to G. retiformis as it

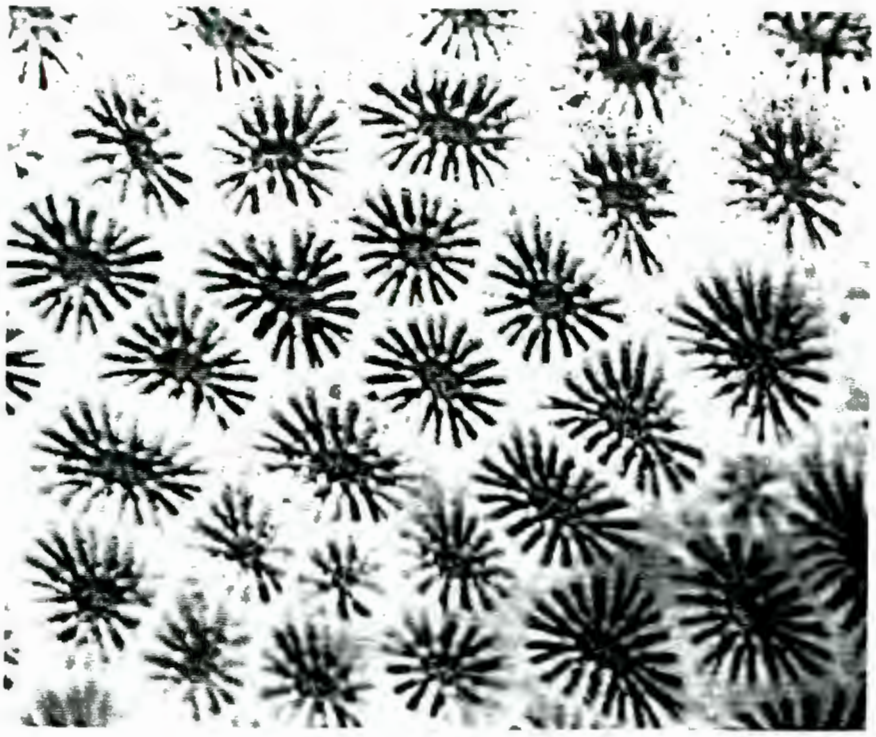


Plate 10a: Goniastrea cf. edwardsi, 2-Mile Reef, South Africa, x2.5.

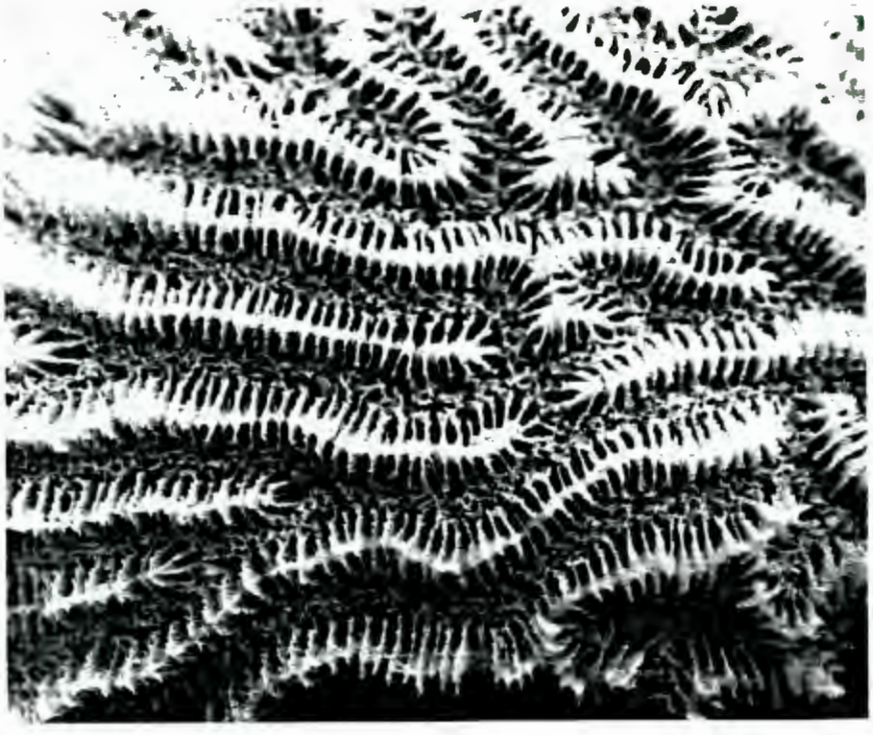


Plate 10b: Platygyra daedalea, 2-Mile Reef, South Africa, x2.

also has small, monocentric and polygonal calices. The corallites, however, appear less angular and the walls are thicker. In addition the septa are thicker, with larger granulations. Septa are exsert and in most corallites continuous over the theca. The size difference between first and second order septa is more pronounced and regular than in the two specimens of G. retiformis. However, more material is needed to confirm the identity of this specimen beyond any doubt.

GENUS PLATYGYRA Ehrenberg, 1834

Generic synonymy

Platygyra Ehrenberg, 1834; Vaughan & Wells (1943); Wells (1956); Chevalier (1971), Veron, Pichon & Wijsman Best (1977).

Astoria Edwards & Haime, 1848.

Coeloria Edwards & Haime, 1848; Matthai (1928); Crossland (1952); Alloiteau (1957).

Characters

Meandroid. Colony formation by linear, intramural, polystomodeal budding. Thecae are narrow and those of adjacent valleys are fused.

PLATYGYRA DAEDALEA (Ellis & Solander, 1786)

(Plate 10b)

Synonymy

Madrepora daedalea Ellis & Solander, 1786.

Meandrina daedalea (Ellis & Solander); Dana (1846).

Astoria daedalea (Ellis & Solander); Edwards & Haime (1849).

Coeloria daedalea (Ellis & Solander); Verrill (1864); Brueggemann (1879b); Studer (1888); Crossland (1952).

Platygyra daedalea (Ellis & Solander); Pichon (1964); Chevalier (1975); Wijsman-Best (1972); Faure (1977); Veron, Pichon & Wijsman-Best (1977); Wijsman-Best, Faure & Pichon (1980); Scheer & Pillai (1983); Veron (1986); Sheppard (1987); Veron & Marsh (1988); Sheppard & Sheppard (1991).

Material examined

11 specimens from Two-Mile Reef, Central Reef Complex, RSA (SAM-H-4656 , ORI/S2/2-4-5/2, SAM-H-4653 , SAM-H-4652 , ORI/S2/2-9-10/6, ORI/S2/2-10-11/2, ORI/S2/2-11-12, ORI/S2/2-13-14/1, ORI/S2/2-13-14/22, ORI/S2/2-15-16/15, ORI/S2A/Fp1), 4 specimens from Inhaca Island, Mozambique (ORI/CVIm1(1), ORI/CVIm1(2), ORI/CVIm2(1), ORI/CVIm2(2) all from Baixo 213).

Corallum

Massive, flat to hemispherical.

Corallites

Meandroid; long, deep valleys, marked centres only at the end of the valleys or in very short series.

Septa

In one to two orders, most septa more or less equal, exsert, septa of neighbouring valleys fuse; above the theca and at the bases of the septa a fine trabecular linkage between the septa; well developed dentations; paliform lobes usually absent.

Columella

Well developed, trabecular, spongy, development varies within the colony.

Thecae

Narrow, often perforated in the upper part.

Observations

The 11 specimens from South Africa form a very homogeneous series in growth form and sceletal characteristics. All were collected in depths less than 20m on Two-Mile Reef, an area with relatively uniform environmental conditions, and represent the same ecotype. All specimens show a tendency to form very long valleys without centres. In the two smallest colonies (ORI/S2/2-13-14/1, ORI/S2A/Fp1) valleys are short, many are mono- to tricentric, but a tendency to form longer valleys is discernible.

Valleys are in most specimens fairly straight, in ORI/S2/2-4-5/24 markedly undulating. The walls are uniformly thin in all specimens. Paliform lobes are not present in any specimen.

The specimens correspond well to the description of "P. daedalea from biotopes with relatively poor illumination" in Veron et al. (1977). ORI/S2/2-4-5/24 resembles the variation "leptotricha" of Chevalier (1971).

Boshoff (1981) identied his specimens from Mozambique as P.lamellina (Ehrbg.). I consider them to be P. daedalea (Ell. & Sol.).

PLATYGYRA SINENSIS (Edwards & Haime, 1849)

(Plate 11a)

Synonymy

Astroria sinensis Edwards & Haime, 1849.

Coeloria sinensis Edwards & Haime, 1857; Studer (1881); Ortmann (1892); Gardiner (1899

Platygyra sinensis (Ed.& H.); Wells (1954); Chevalier (1975); Scheer & Pillai (1983); Veron, Pichon & Wijsman Best (1977); Veron (1986); Sheppard (1987); Veron & Marsh (1988); Sheppard & Sheppard (1991).

Material examined

2 specimens from Bassas da India, Lagoon (ORI/BdI/1991-8-48, ORI/BdI/1991-8-49).

Corallum

Massive, spherical.

Corallites

Meandroid in short series, mostly one to three corallites per series, diameter 4-6 mm.

Septa

Thin, hardly to only slightly exsert, no differentiation into distinct size classes, most meet the columella, evenly spaced, well developed dentations, no paliform lobes, sides slightly granulated.

Columella

Well developed, of twisted trabeculae which can fuse to form vertical plates.

Thecae

Thin.

Observations

This species is apparently absent from the African mainland coast. It is easily distinguished from P. daeadalea by the shorter series, the smaller corallites and the narrow thecae. It is close to P. pini, which can be distinguished by the much thicker walls.

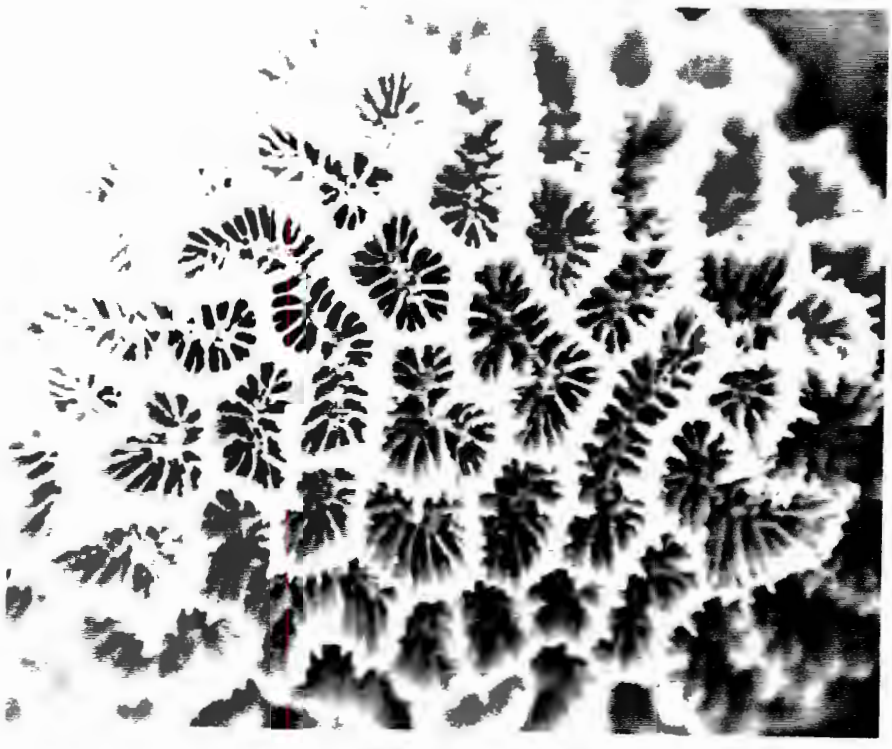


Plate 11a: Platygyra sinensis, Bassas da India, x2.5.

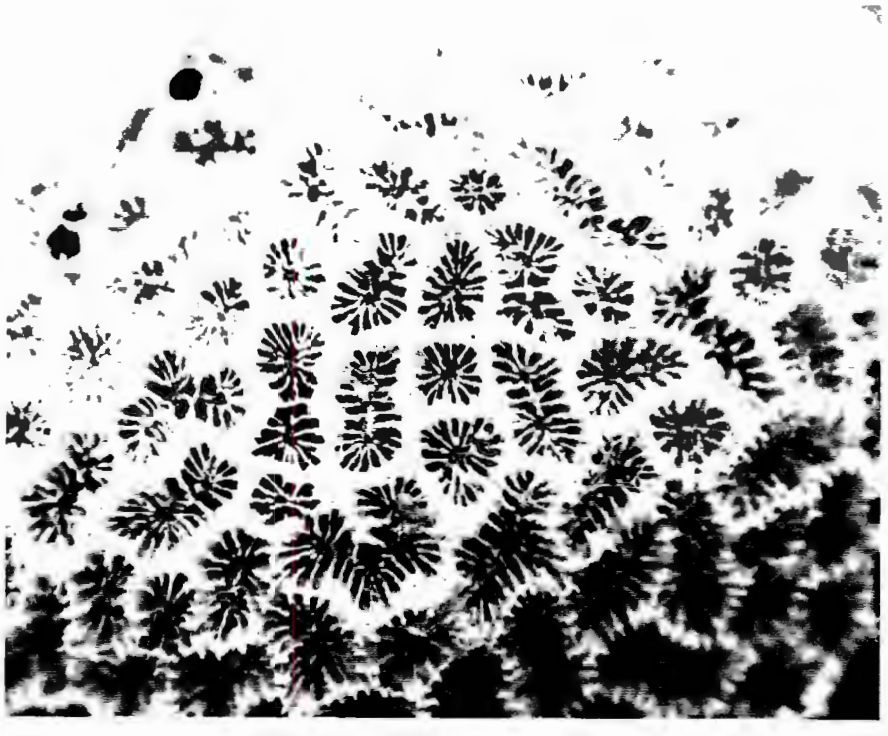


Plate 11b: Platygyra crosslandi, Bassas da India, x2.

PLATYGYRA CROSSLANDI (Matthai, 1928)

(Plate 11b)

Synonymy

Platygyra crosslandi Matthai (1928); Scheer & Pillai (1983); Sheppard (1987); Sheppard & Sheppard (1991).

?Platygyra pini (Chevalier, 1975); Wijsman-Best (1976); Veron, Pichon & Wijsman-Best (1977); Veron (1986); Sheppard (1987).

Material examined

2 specimens from Bassas da India, Lagoon (ORI/BdI/1991-8-50, ORI/BdI/1991-8-51).

Corallum

Massive, hemispherical.

Corallites

Meandroid, mono to polycentric, longest series with up to 4 centres, diameter 3-5 mm.

Septa

No differentiation into regular size classes, well developed dentations, septal sides and dentations granulated, paliform lobes made up of fused septal teeth may be present (BdI/1991-8-50), most septa meet the columella; exsert, septa af neighbouring corallites fuse over the thecae.

Columella

Well developed, spongy, incorporating septal teeth.

Thecae

Very well developed, thick.

Observations

This is another species which seems absent from SE-Africa, although present at Bassas da India. It is close to P. sinensis

and P. pini as both species have very short series. P. crosslandi and P. pini have much thicker walls, a better developed columella, bigger septal dentations and paliform lobes, which are missing in P.sinensis. The species' characters and the illustrations and descriptions in Scheer & Pillai (1983) and Sheppard & Sheppard (1991) seem to indicate that P. crosslandi may be synonymous with P. pini (Matthai, 1928). However, more material is needed to confirm this point.

GENUS LEPTORIA Edwards & Haime, 1848

Generic synonymy

Madrepora Ellis & Solander, 1786.

Meandrina (pars) Dana, 1846.

Leptoria Edwards & Haime, 1848; Vaughan (1918); Matthai (1924); Vaughan & Wells (1943); Wells (1956); Chevalier (1971); Veron, Pichon & Wijsman Best (1977).

Platygyra (pars) Matthai (1928); Yabe, Sugiyama & Eguchi (1936).

Characters

Meandroid. Colony formation by intramural, polystomodeal budding. Thecae thin, septothecal. Columella thin, lamellar, continuous to not continuous.

LEPTORIA PHRYGIA (Ellis & Solander, 1786)

(Plate 12a)

Synonymy

Madrepora phrygia Ellis & Solander, 1786.

Meandrina phrygia (Ellis & Solander); Dana (1846).

Leptoria phrygia (Ellis & Solander); Edwards & Haime (1857); Bernard (1900); von Marenzeller (1901); Vaughan (1918); Wells (1950); Crossland (1952); Chevalier (1975); Wijsman-Best (1972, 1976); Scheer & Pillai (1974); Faure (1977); Veron, Pichon & Wijsman-Best (1977); Wijsman-Best, Faure & Pichon (1980) Scheer & Pillai (1983); Veron (1986); Sheppard (1987); Veron & Marsh (1988); Veron (1990); Sheppard & Sheppard (1991).

Material examined

2 specimens from Inhaca Island, Mozambique (ORI/CVIm3(1) from Baixo 213, ORI/CVIm3(2) from Pta. Rasa), 1 specimen from Bassas da India, Lagoon (ORI/BdI/1991-8-38).

Corallum

Submassive to massive, flat to hemispherical.

Corallites

Meandroid, very regular, deep valleys of indefinite length.

Septa

Mostly in one order, smaller septa interspersed infrequently, connected to the columella by lobes, exsert, septa of neighbouring valleys join over the thecae, finely granulated.

Columella

Well developed, continuous in form of a vertical plate.

Thecae

Thick and dense.

Observations

This species is easy to seperate from all Platygyra by the regular arrangement of the valleys and septa and the well developed, platelike columella.

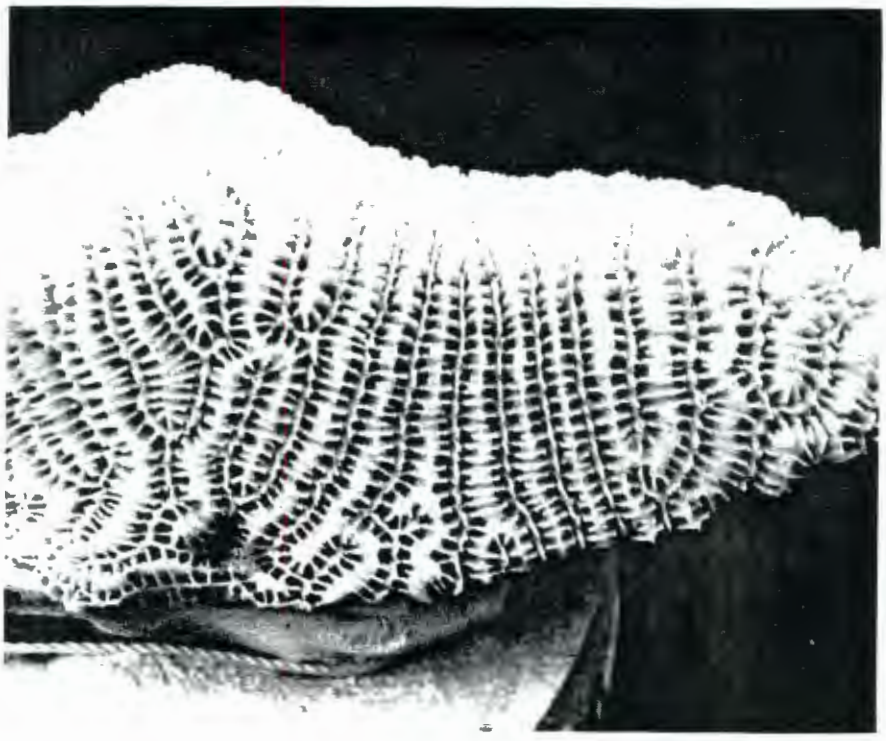


Plate 12a: Leptoria phrygia, Inhaca Island, Mozambique, x2.5.

Plate 12b: Oulophyllia crispa, Inhaca Island, Mozambique, x0.75.

Only beached fragments have been found in South Africa; no live specimens have yet been recorded.

GENUS OULOPHYLLIA Milne Edwards & Haime, 1848

Generic synonymy

Meandrina (pars) Lamarck, 1816.

Oulophyllia Edwards & Haime, 1849.

Ulophyllia Edwards & Haime, 1857.

Coeloria (pars) Gardiner, 1904.

Coelogyra Nemenzo, 1959.

Characters

Similar to Favites, but meandroid. Colony formation by intramural, polystomodeal budding. Valleys are wide, rather short and often discontinuous. Distinct centres are usually present.

OULOPHYLLIA CRISPA (Lamarck, 1816)

(Plate 12b)

Synonymy

Meandrina crispa Lamarck, 1816; de Blainville (1823, 1830, 1834); Edwards & Haime (1848).

Ulophyllia crispa Edwards & Haime, 1857; Verrill (1901).

Ulophyllia aspera Quelch, 1886.

Oulophyllia crispa Matthai, 1928; Yabe, Sugyama & Eguchi (1936); Crossland (1952); Wijsman-Best (1972, 1976); Pillai & Scheer (1976); Faure (1977); Veron, Pichon & Wijsman-Best (1977); Wijsman-Best, Faure & Pichon (1980); Scheer & Pillai (1983); Veron (1986); Sheppard (1987); Veron & Marsh, 1988; Sheppard & Sheppard (1991).

Oulophyllia aspera Matthai, 1928; Scheer & Pillai (1974); Chevalier (1975); Wijsman-Best (1976).

Material examined

3 specimens from Inhaca Island, Mozambique (ORI/CVI11(1), ORI/CVI12(1), ORI/CVI12(2)).

2 specimens from Two-Mile Reef, Central Reef Complex, RSA (not indexed).

Corallum

Massive, hemispherical.

Corallites

Meandroid, with distinct centres, valley width 8-15 mm, valleys with up to 8 centres.

Septa

Thin, in two orders although they cannot always be distinguished; exsert; first order septa more exsert than those of the second order, which are sometimes obsolete in their upper part where they fuse with the wall; septa from neighbouring valleys join over the thecae; sides with granules arranged in rows; conspicuous dentations increasing in size towards the centres of the valleys.

Columella

Well developed, spongy; columellae from adjacent centres are connected by a trabecular network incorporating twisted septal teeth, sometimes with platelike anastomoses.

Thecae

Thin, perforate in their uppermost partions.

Observations

This species is easily recognized by its wide valleys, being the only meandroid species with such large corallites in the area. It

is very common, especially in areas of high sedimentation. I consider Boshoff's (1981) O. aspera Quelch to also be O. crispa (Lam.).

GENUS MONTASTREA de Blainville, 1830

Generic synonymy

Montastrea de Blainville, 1830; Wells (1956); Chevalier (1971); Veron, Pichon & Wijsman Best (1977).

Orbicella Dana, 1846.

Heliastrea Edwards & Haime, 1857.

Characters

Since the treatment of this genus by Chevalier (1971) it has been widely accepted that Montastrea is not an exclusively Atlantic genus as was previously maintained by Wells (1956). It is a difficult genus, as it is hard to distinguish, especially from Plesiastrea (Chevalier, 1971, Veron et al., 1977). Colony formation is by extratentacular budding, septa are dentate but without true pali.

MONTASTREA ANNULIGERA (Edwards & Haime, 1849)

(Plate 13a)

Synonymy

Orbicella anulligera Edwards & Haime, 1849.

Montastrea annuligera (Edwards & Haime); Wijsman-Best (1977); Veron, Pichon & Wijsman-Best (1977); Wijsman-Best, Faure & Pichon (1980); Veron (1986); Sheppard (1987); Veron & Marsh (1988); Antonius, Scheer & Bouchon (1990).

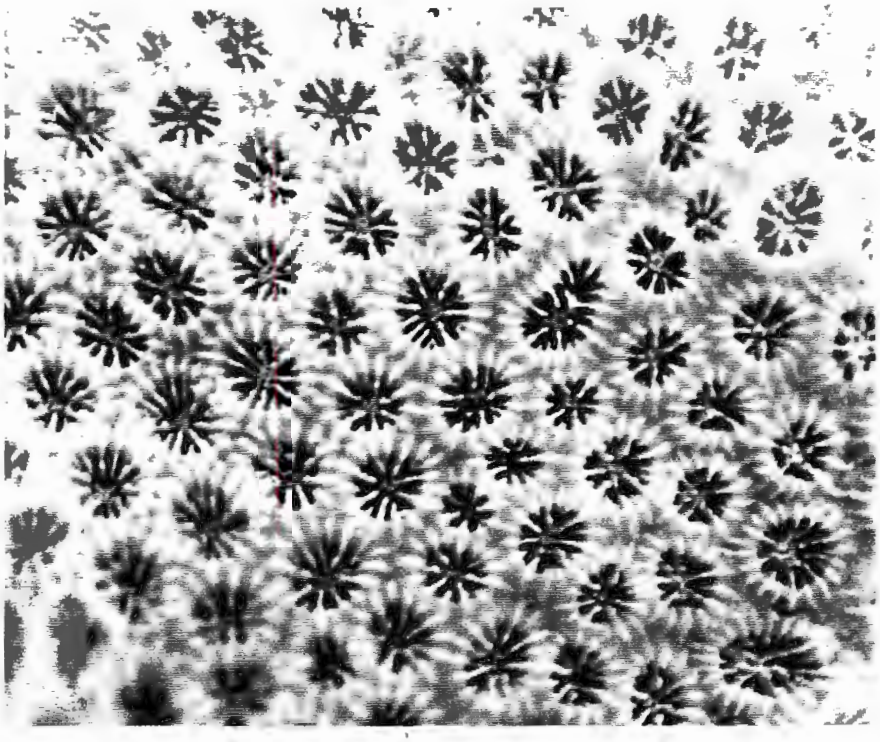


Plate 13a: Montastrea annuligera, Inhaca Island, Mozambique, x2.5.

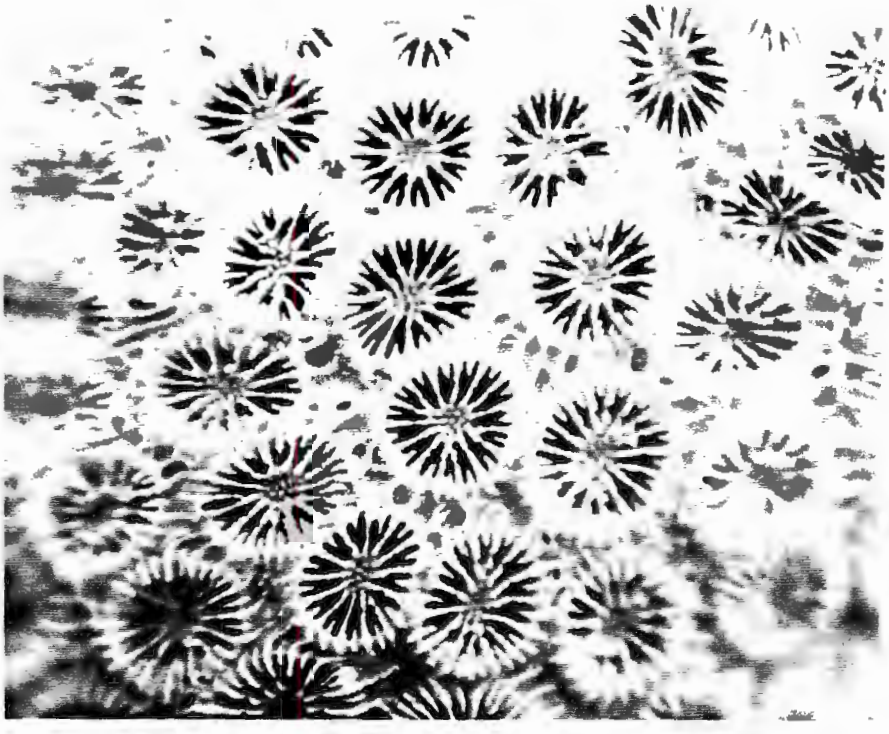


Plate 13b: Montastrea curta, Inhaca Island, Mozambique, x2.5.

Material examined

1 specimen from Umdloti, Natal (ORI/CVIk1(4)).

Corallum

Massive, columnar.

Corallites

Diameter 2.2-3 mm, very uniform in size, round to elongate where crowded, never polygonal, about 1 mm exsert, separated by a well formed groove.

Septa

In three cycles; first order markedly thickened above the theca, reach the columella, dentate, sides granulated, with paliform lobe, which is fused to the columella; second cycle mostly does notreach the columella, thickened above the theca, with paliform lobe, often fused to first cycle septa, dentate, sides granulated; third order septa very small.

Columella

Short and deep inside the calyx but well developed, spongy.

Costae

Equal to subequal, do not run onto the coenosteum.

Observations:

This species can often be observed in tidal pools on theNatal North Coast. Boshoff erronously identified his specimen from Mozambique as M. annularis (Ell. & Sol.), an Atlantic coral. This identification requires further verification.

MONTASTREA CURTA (Dana, 1849)

(Plate 13b)

Synonymy:

Orbicella curta Dana, 1846; Gardiner (1899); Vaughan (1917, 1918);

Yabe & Sugiyama (1935); Crossland (1952).

Montastrea curta (Dana); Chevalier (1971); Faure (1977); Wijsman-Best (1977); Veron, Pichon & Wijsman-Best (1977); Veron (1986); Sheppard (1987); Veron & Marsh (1988); Veron (1990); Sheppard & Sheppard (1991).

Material examined

3 specimen from Inhaca Island, Mozambique (ORI/CVIk1(3) from Pta.Torres; ORI/CVIk2(1) and ORI/CVIk2(2) from Cabo Inhaca).

Corallum

Massive, hemispherical.

Corallites

Round, regular, diameter 3.5-6 mm, well spaced, exsert to about 1 mm.

Septa

In three cycles, the first two of same size and shape, not, to only slightly, thickened above the thecae, exsert, reach the columella, with paliform lobes which are fused to the columella, mostly small, regular dentations or large, ornamented spines, sides granulated; third cycle only to 1/3-1/2R, septa descend abruptly into the calyx, do not reach the columella, exsert, sides granulated.

Columella

Well developed, of upright and only partly fused trabeculae.

Costae

First and second cycle costae are of same size but bigger than third cycle costae; first and second cycle run onto the coenosteum, third cycle doesn't.

Coenosteum

Blistered.

Observations

This species is easily separated from M. annuligera by the larger size of the costae, the presence of only two size classes of septa and the fact that the costae run onto the coenosteum. Corallites are more widely spaced than in the M. annuligera specimens. No records from South Africa are available for this species. Boshoff (1981) called his specimens M. aperta (Verrill).

GENUS PLESIASTREA Edwards & Haime, 1848

Generic synonymy

Astraea (pars) Lamarck (1816).

Plesiastrea Edwards & Haime (1848).

Orbicella (pars) Vaughan, 1907; Yabe, Sugiyama & Eguchi (1936).

Favia (pars) Matthai (1914).

Characters

Very similar to Montastrea, distinguished by the presence of true pali.

PLESIASTREA VERSIPORA (Lamarck, 1816)

(Plate 14a)

Synonymy

Astraea versipora Lamarck, 1816.

Orbicella versipora (Lamarck); Gardiner (1899); Vaughan (1918); Yabe & Sugiyama (1935).

Plesiastrea versipora (Lamarck); Edwards & Haime (1849, 1857); Crossland (1952); Wells (1954); Chevalier (1971); Pillai & Scheer

(1973); Scheer & Pillai (1974); Wijsman-Best (1977); Veron, Pichon & Wijsman-Best (1977); Wijsman-Best, Faure & Pichon (1980); Scheer & Pillai (1983); Veron (1986); Sheppard (1987); Veron & Marsh (1988); Veron (1990); Sheppard & Sheppard (1991).

Material examined

3 specimens from Two-Mile Reef, Central Reef Complex, RSA (ORI/S2/1991-2-14 , ORI/S2/1991-2-15), 1 specimen from Nine-Mile Reef, Central Reef Complex, RSA (ORI/S9/1992-1-16), 2 specimens from Inhaca Island, Mozambique (ORI/CVIn2(3) from Baixo 213, ORI/CVIk1(2) from Saco da Inhaca).

Corallum

Massive, with or without laminar edges.

Corallites

Plocoid, diameter 2-3 mm, crowded, round to slightly polygonal where crowded.

Septa

In three orders, the first two may be of the same size, third order much smaller, true pali on first and second order, forming mostly one, in some corallites two concentric crowns of pali around the columella; pali thickened; septa of first and second order project horizontally into the calyx for about 2/3R, then descend abruptly; septa moderately exsert, thickened over the thecae.

Columella

Weakly developed, consisting of only a few rod-like trabeculae.

Costae

Equal to subequal, do not run far into the coenosteum, usually separated by an intercalicular groove.

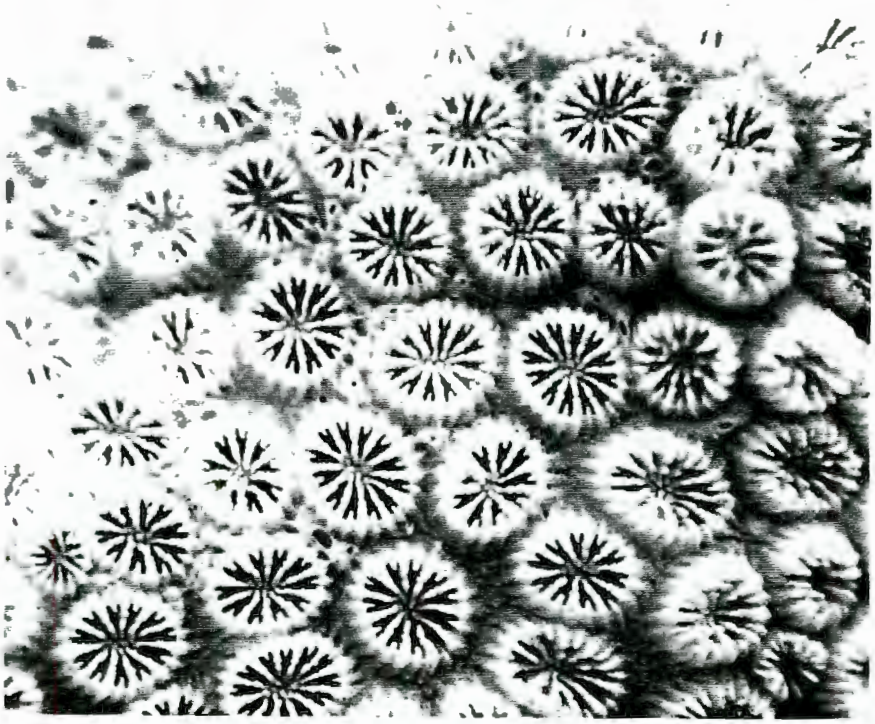


Plate 14a: Plesiastrea versipora, Inhaca Island, Mozambique, x3.

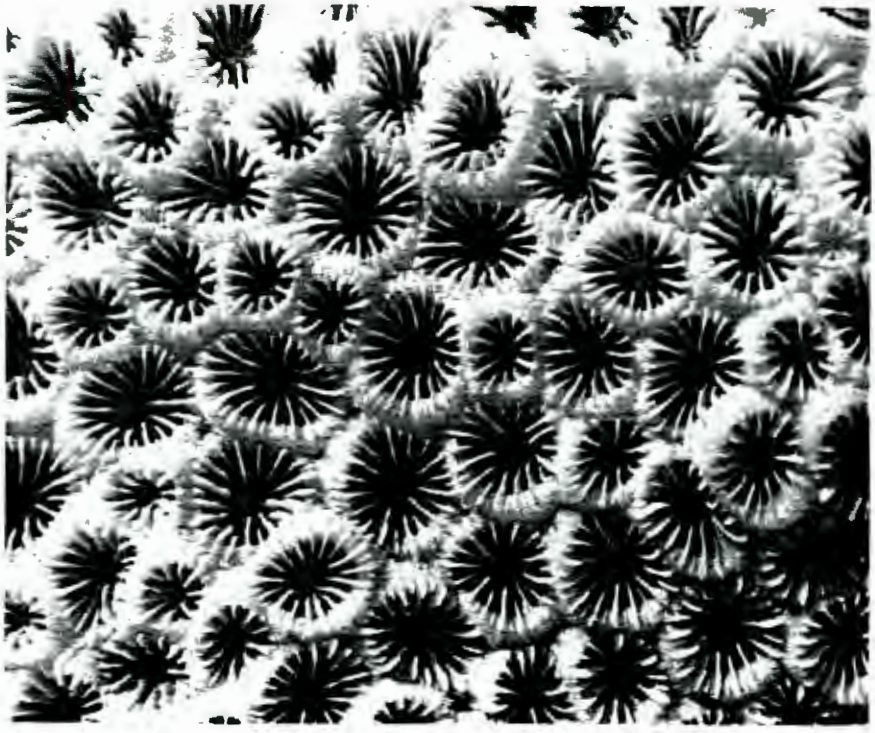


Plate 14b: Leptastrea purpurea, Inhaca Island, Mozambique, x2.5.

Observations

The specimens correspond very well to the description of ecomorph "urvillei" of Veron et al. (1977). The original colony, from which the specimens ORI/S2/1991-2-14 and ORI/S2/1991-2-15 were taken, was massive with laminar edges growing in layers.

P. versipora is very similar in appearance to some Montastrea. They can, however, be separated by the form of their septa and the development of the pali (in Plesiastrea) or paliform lobes (in Montastrea). The true pali in Plesiastrea are much larger then the paliform lobes of Montastrea. Also the septa of Plesiastrea do not descend as abruptly into the calyx as in Montastrea. The living colony is often very attractively colored, with a white coenosarc and red polyps with white oral disc.

Boshoff (1981) erronously identified his specimens from Mozambique as Montastrea annularis (Ell.& Sol.), an Atlantic species.

GENUS LEPTASTREA Edwards & Haime, 1848

Generic synonymy

Leptastrea Edwaeds & Haime, 1848.

Baryastrea Edwards & Haime, 1848.

Characters:

This genus is close to Montastrea and the two are often difficult to distinguish. In most southern African specimens Leptastrea has smaller, less exsert corallites. These are primarily rounded, but as they are usually crowded, they tend to become more irregular in shape. Septa are in two or more size classes. The columella is well developed and consists of rod-like trabeculae. Paliform lobes may, or may not be developed.

LEPTASTREA cf. PURPUREA (Dana, 1846)

(Plate 14b)

Synonymy

Astraea purpurea Dana, 1846.

Leptastrea purpurea (Dana); Hoffmeister (1925, 1929), Crossland (1948, 1952); Chevalier (1975); Veron, Pichon & Wijsman-Best (1977); Wijsman-Best, Faure & Pichon (1980); Scheer & Pillai (1983); Veron (1986); Sheppard (1987); Veron & Marsh (1988); Sheppard & Sheppard (1991).

Leptastrea ehrenbergana Edwards & Haime, 1848; Crossland (1952); Boshoff (1981).

Material examined

2 specimens from Inhaca Island, Mozambique ORI/CVIn2(1) from Pta. Rasa, ORI/CVIn1(1) from Cabo Inhaca); 1 specimen from Umdloti, Natal (ORI/CVIj2(1)).

Corallum

Encrusting.

Corallites

Round to polygonal, diameter up to 4 mm.

Septa

In three cycles of which the first two may be indistinguishable; first cycle exsert, reaches the columella, paliform lobes, granulated sides, not to slightly thickened above the theca; second cycle less exsert than first cycle, does not reach the columella, no paliform lobes, granulated sides; third cycle reduced.

Columella

Well developed, often fuses with paliform lobes of the first septa

cycle.

Costae

Poorly developed or absent.

Observations

As the species in this genus are very variable and difficult to distinguish, there remains some incertainty to the identity of this specimen. More specimens would be needed in order to allow further insights into the variability and therefore a more certain identification.

Boshoff (1981) erronously identified one specimen as Solenastrea hyades (Dana), an Atlantic species. Solenastrea is now considered to be, at least partly, a synonym of Cyphastrea (Veron et al. 1977).

LEPTASTREA BOTTAE (Edwards & Haime, 1849)

Synonymy

Cyphastrea bottae Edwards & Haime, 1848.

Cyphastrea bottai Milne Edwards & Haime, 1857.

Leptastrea bottai Ortmann (1888)

Leptastrea inaequalis Klunzinger, 1879; Veron, 1986.

Leptastraea bottae Klunzinger, 1879; Vaughan (1918); Crossland (1948, 1952); Veron, Pichon & Wijsman-Best (1977); Scheer & Pillai (1983); Sheppard (1987), Veron (1990).

Material examined

1 specimen from Inhaca Island, Mozambique (ORI/CVIn2(2)).

Corallum

Massive.

Corallites

Round, exsert to 1 mm, diameter around 3 mm.

Septa

In three orders; the first two orders often indistinguishable; first order septa reach the columella, the paliform lobes often being integrated into the columella; very fine dentations, sides smooth to finely granulated; exsert, thickened above the theca; second order septa generally do not reach the columella, usually without paliform lobe, smoothe to very finely granulated, less exsert than first order septa; third order septa reduced.

Columella

Well developed, consisting of trabeculae and twisted paliform lobes.

Costae

Septocostae thickened, in two orders corresponding to the the septal orders.

Coenosteum

With fine dentations.

Observations

There remains room for doubt whether the identification of this single specimen is correct. More specimens would be needed for confirmation.

GENUS CYPHASTREA Edwards & Haime, 1848

Generic synonymy

Cyphastrea Edwards & Haime, 1848; Chevalier (1971); Veron, Pichon & Wijsman Best (1977).

Solenastrea (pars) Edwards & Haime, 1848.

Characters

This genus is easily identified by the small size of the corallites (mostly around 3 mm), which are usually round and not crowded, and the two very distinct size classes of the septa. Corallites are usually plocoid and in many species well spaced. The coenosteum is blistered and/or covered with spinules. Septa are very distinct - a cycle of 12 large septa is alternating with 12 small septa, which do not reach the columella. The large septa are often thickened above the thecae, which gives them an arrow-shaped appearance.

CYPHASTREA CHALCIDICUM (Forskal, 1775)

(Plate 15a)

Synonymy

Madrepora chalcidicum Forskal, 1775.

Cyphastrea chalcidicum (Forskal); Klunzinger (1879); Ortmann (1888, 1892); Crossland (1952); Yabe & Sugiyama (1935); Rosen (1971); Veron, Pichon & Wijsman-Best (1977); Boshoff (1981); Veron (1986); Sheppard (1987); Veron & Marsh (1988).

Material examined

3 specimens from Inhaca Island, Mozambique (ORI/CVIc1(1), ORI/CVIc1(3) from Pta. Torres, ORI/CVIc1(4) from Pta Rasa).

2 specimens from the Northern Reef Complex off Kosi Mouth, RSA (ORI/KB/1991-9-43, ORI/KB/1991-9-44).

Corallum

Massive.

Corallites

Small, conical, exsert, diameter up to 2 mm.

Plate 15a: Cyphastrea chalcidicum, Inhaca Island, Mozambique, x4.

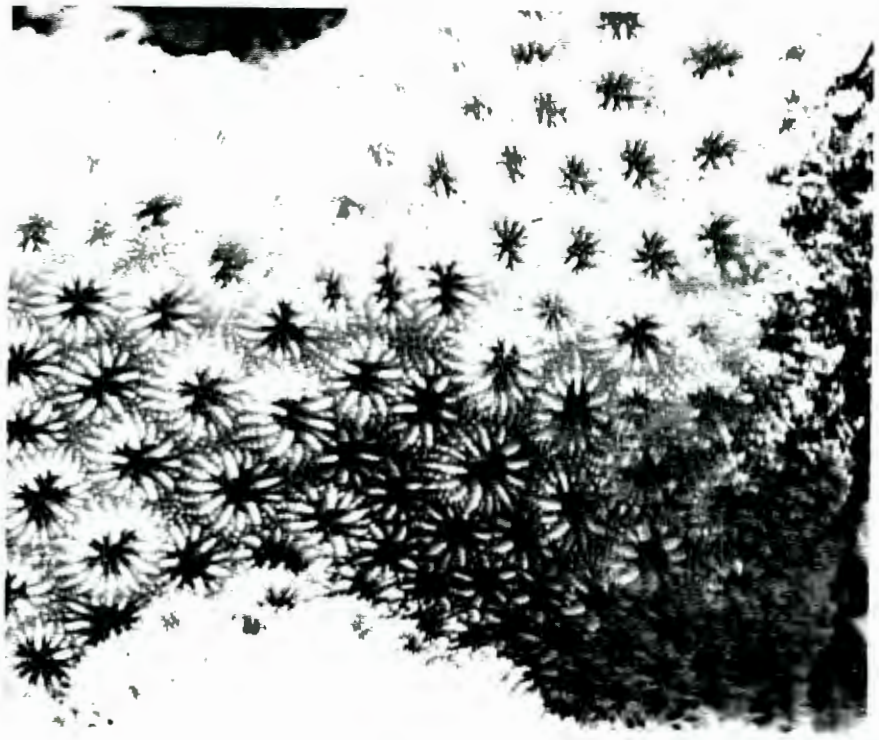


Plate 15b: Cyphastrea serailia, Bassas da India, x7.5.

Septa

24 in two orders; first order large and thick, sometimes divided into two hexameral cycles where the primary cycle is 1/4 bigger than the secondary cycle; septal sides granulated; no paliform lobes; second order reduced.

Columella

Weakly developed, consists of only a few twisted trabeculae.

Costae

First order well developed, second order markedly smaller.

Coenosteum

Blistered, with exothecal spines.

Observations

This is the only species of Cyphastrea so far recorded on the South East African mainland coast. Corallites are slightly smaller and thecae thinner then in the C. serailia specimens from Bassas da India. Also the coenosteum is more blistered with less spines in the C. chalcidicum specimens.

CYPHASTREA SERAILIA (Forskal, 1775)

(Plate 15b)

Synonymy

Madrepora serailia Forskal, 1775.

Cyphastrea serailia (Forskal); Ortmann (1888); Vaughan (1918); Yabe & Sugiyama (1935); Crossland (1952); Wells (1954); Chevalier (1975); Faure (1977); Veron, Pichon & Wijsman-Best (1977); Wijsman-Best, Faure & Pichon (1980); Scheer & Pillai (1983); Veron (1986); Sheppard (1987); Veron & Marsh (1988); Veron (1990); Sheppard & Sheppard (1991).

Material examined

2 specimen from Bassas da India, Lagoon (ORI/BdI/1991-8-52, ORI/BdI/1991-8-53).

Corallum

Massive, spherical.

Corallites

Round, some conical and exsert, diameter up to 3.5 mm.

Septa

24 in two orders; first order markedly bigger and thicker, differentiated into two cycles of different size, paliform lobes present, big dentations, reach the columella; second order reduced, no paliform lobes, do not reach the columella; septal sides strongly granulated.

Columella

Well developed, trabecular.

Costae

First and second order of equal size.

Coenosteum

Covered with strong, ornamented spines.

Thecae

Very variable, either thick and well exsert or confluent with the coenosteum.

Observations

This species differs from C. chalcidicum by the presence of paliform lobes and usually has a thicker wall. It has only been recorded from Bassas da India. The specimens resemble the variation "ocellina" in Chevalier (1975). Boshoff (1981) called his specimens from Mozambique Solenastrea spongiformis Duncan,

this genus is considered to be synonymous with Cyphastrea (see above).

GENUS ECHINOPORA Lamarck, 1816

Generic Synonymy

Echinopora Lamarck, 1816.

Explanaria Lamarck, 1816; (pars) Ehrenberg, 1834.

Echinastrea de Blainville, 1830.

Stephanocora Ehrenberg, 1834.

Acanthophora Verrill, 1864.

Acanthelia Wells, 1937.

Characters

Echinopora is closest to Cyphastrea from which it is separated by bigger corallites and a mostly lamellar, fruticose or submassive growth form, while Cyphastrea typically grows massive.

ECHINOPORA LAMELLOSA (Esper, 1795)

(Plate 16a)

Synonymy

Madrepora lamellosa Esper, 1795.

Echinopora concinna Verrill, 1901; Boshoff (1981).

Echinopora lamellosa (Esper); Vaughan (1918); Crossland (1952); Wells (1954); Scheer & Pillai (1974); Chevalier (1975); Pillai & Scheer (1976); Faure (1977); Veron, Pichon & Wijsman-Best (1977); Wijsman-Best, Faure & Pichon (1980); Scheer & Pillai (1983); Veron (1986); Sheppard (1987); Veron &Marsh (1988); Veron (1990); Sheppard & Sheppard (1991).

Material examined

1 specimens from Inhaca Island, Mozambique (ORI/CVId1(1), 1 specimen from Xai Xai, Mozambique coast (ORI/CVId1(2)).

Corallum

Laminar, expanding horizontally.

Corallites

Diameter around 4 mm, well spaced, equally exsert.

Septa

In three cycles; first cycle marginally thicker than the others, exsert, with prominent spines and often lobes, paliform lobes present, sides granulated; second cycle thinner less exsert, with paliform lobes, sides granulated; third cycle incomplete in some corallites, does not reach the columella.

Columella

Well developed, spongy.

Costae

Well developed, equal to subequal with numerous, equally spaced prominent spines.

Observations

This species is easily distinguishable from all other Echinopora by the laminar growth form, the smaller size of the corallites and dentations. The difference between the first and second septal cycle is not as pronounced as in other Echinopora, also the columella is less compact. E. lamellosa seems to have its southern distribution limit at Inhaca Island in Mozambique as it has not been recorded in South Africa yet.

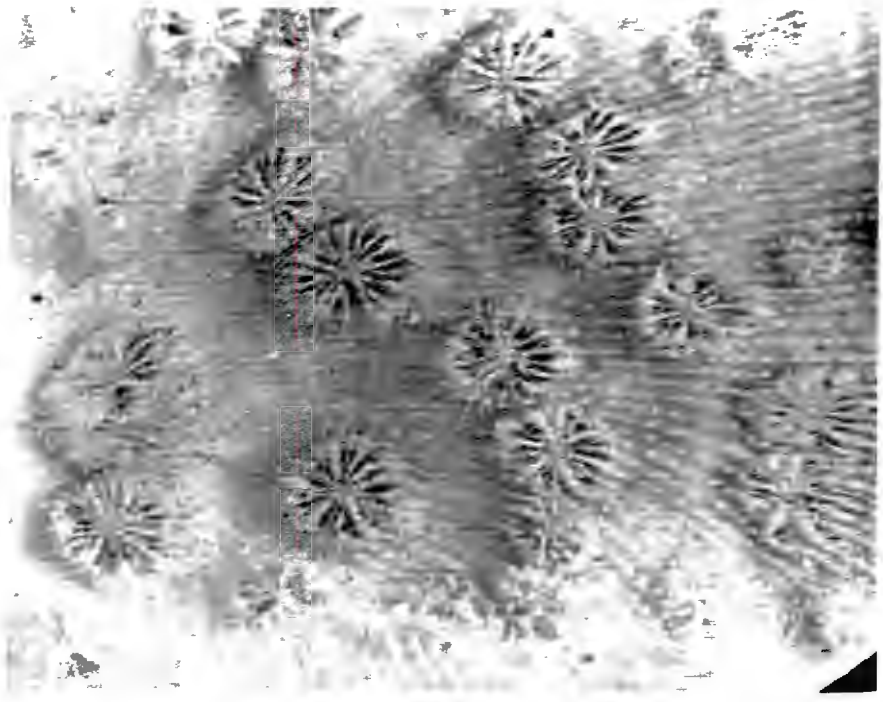


Plate 16a: Echinopora lamellosa, Inhaca Island, Mozambique, x5.

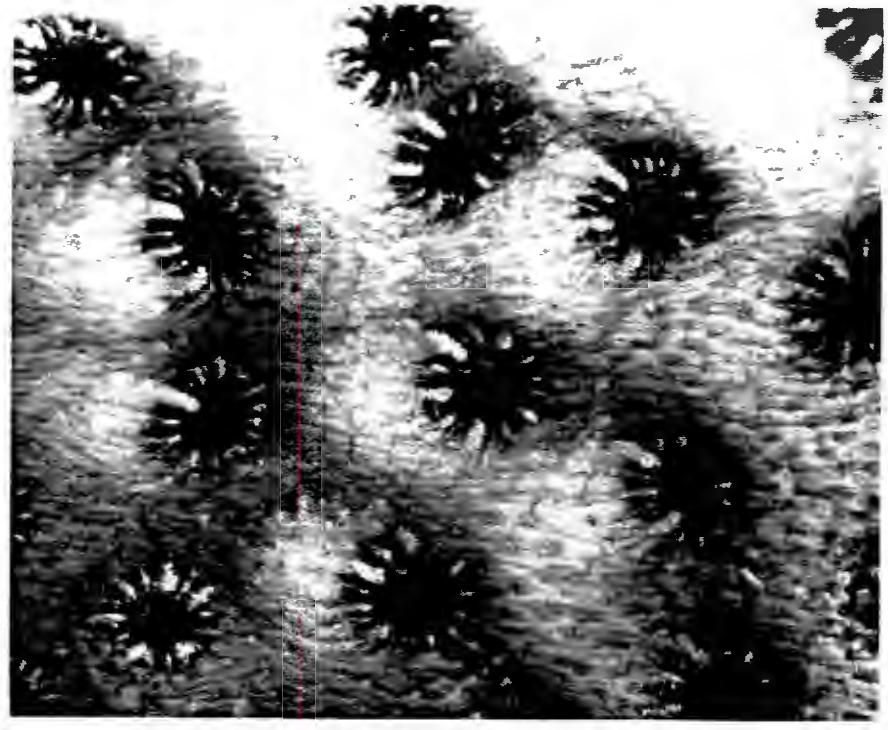


Plate 16b: Echinopora gemmacea, Bassas da India, x5.

ECHINOPORA GEMMACEA (Lamarck, 1816)

(Plate 16b)

Synonymy

Explanaria gemmacea Lamarck, 1816.

Echinastrea gemmacea (Lamarck); de Blainville (1830, 1834).

Echinopora gemmacea (Lamarck); Edwards & Haime (1849); Chevalier (1975); Faure (1977); Veron, Pichon & Wijsman-Best (1977); Wijsman-Best, Faure & Pichon (1980); Scheer & Pillai (1983); Veron (1986); Sheppard (1987); Veron & Marsh (1988); Sheppard & Sheppard (1991).

Echinopora fruticulosa Klunzinger, 1879. Sheppard & Sheppard (1991).

Material examined:

3 specimens from Inhaca Island, Mozambique (ORI/CVId2(2), ORI/CVId2(3), ORI/CVId3(2)), 1 specimen from Two-Mile Reef, Central Reef Complex, RSA (ORI/S2/1991-6-2), 1 specimen from Nine-Mile Reef, Central Reef Complex, RSA (ORI/S9/1991-2-8), 2 specimens from Bassas da India, Lagoon (ORI/BdI/1991-7-23, ORI/BdI/1991-7-25).

Corallum

Lamellar with ramose proliferations to submassive and flat without any proliferations.

Corallites

Immersed to markedly exsert, diameter up to 8 mm.

Septa

Three cycles; first cycle the thickest, thinning towards the centre, very exsert, with prominent lobe above the theca, which is rarely devided into two lobes, prominent paliform tooth, reaches

the columella; second cycle thinner than first, less exsert, reaches the columella; third cycle often reduced, does not reach the columella.

Columella

Well developed, spongy.

Costae

Well developed, exothecal costae often incompletely fused, ornamented costal spines.

Observations

This is a very common species on South African reefs. It is also the most common Echinopora. The typical growth form is lamellar, rarely producing more than thick upward pointing proliferations. ORI/S9/1991-2-8 is such a proliferation. A more or less branching growth form, as in the variation "fruticulosa", is never developed.

ECHINOPORA HIRSUTISSIMA (Edwards & Haime, 1849)

(Plate 17a)

Synonymy

Echinopora hirsutissima Edwards & Haime, 1849; Chevalier (1975), Pillai & Scheer (1976); Veron, Pichon & Wijsman-Best (1977); Scheer & Pillai (1983); Veron (1986); Sheppard (1987); Veron & Marsh (1988).

Material examined

1 specimen from Inhaca Island, Mozambique (ORI/CVId3(1)), 1 specimen from Bassas da India, lagoon (ORI/BdI/1991-8-54).

Corallum

Laminar.

Corallites

Mostly well exsert, some almost flush with the coenosteum.

Septa

Three complete septal cycles, a rudimentary fourth cycle can be present; primary cycle is the thickest and most exsert, prominent paliform tooth on inner margin, between the dentations of the inner septal margin and the septum proper a series of pores, septum very hirsute with prominent lobes; secondary cycle is thinner and less exsert, reaches the columella; tertiary cycle the smallest, does not always reach the columella.

Columella

Well developed, spongy.

Costae

Well developed, hirsute, exothecal costae subequal with numerous spines.

Thecae

A very well developed exotheca on many corallites, which gives the corallite a rounded, "inflated" appearance.

Observations

The taxonomy of this species is problematic as it is difficult to delineate it and especially difficult to separate it from Echinopora gemmacea. The holotype in the Museum national d'histoire naturelle (Paris) shows a progression of typically hirsutissima-type corallites on the convex parts to almost gemmacea-type corallites on the lower, concave parts. The growth form is however different from E. gemmacea, as it has not been described as forming similar vertical, fruticulose proliferations.

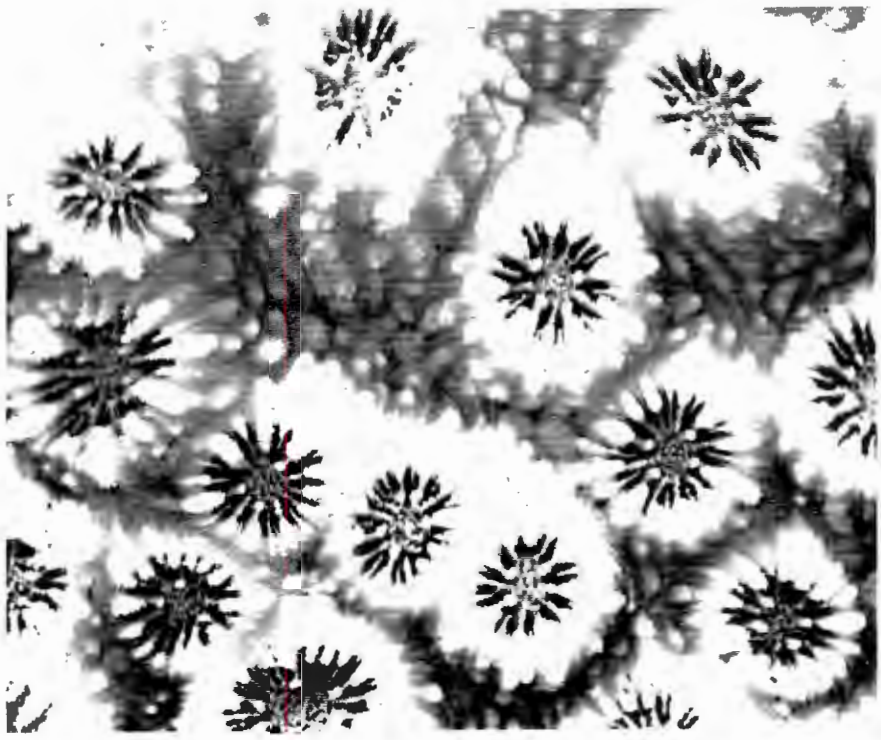


Plate 17: Echinopora hirsutissima, 2-Mile Reef, South Africa, x5.

More material would be needed in order to give an authoritative discussion of its specific status.

Boshoff (1981) identified his specimen from Mozambique as E.carduus Klunz., which is considered by Veron et al. (1977) a synonym of E.gemmacea (Lam.).

Conclusions

The faviid fauna of South East Africa, especially of Northern Natal, was found to be richer than previously recorded (Wijsman-Best et al., 1980; Boshoff, 1980). Of the 28 species faviidae, which were found to occur in this region, most are typical of the tropical Indo-Pacific fauna. The South East African faviid fauna

is similar to that found in most reef areas of the Indian Ocean (Sheppard, 1987). Previous records about the South East African coral fauna, especially those in Boshoff (1981) were not reliable due to numerous misidentifications and taxonomic errors. The common presence of Favia speciosa (Dana) in South East Africa is comparable to the situation in Eastern Australia, where this species is only common south of the Great Barrier Reef (Veron, 1986). Many faviids are found well south of the coral reef area in northern Natal. Favia speciosa, Favites halicora, Plesiastrea versipora and Montastrea annuligera are found in tidal pools in central and southern Natal, where they can form large colonies, especially in central Natal.

The faviid fauna of Mozambique was richer (27 species) than that of South Africa (24 species). There was a further increase in species richness on Bassas da India, with four species, which were not found on the African mainland. Within the study area an increasing loss of species richness is observed with an increasing distance from the Eastern Indian Ocean diversity centre (Rosen, 1988; Jokiel & Martinelli, 1992). Compared with other areas in the Indian Ocean, the South East African faviid fauna is only moderately rich, compared to 42 species in the Arabian region (Sheppard & Sheppard, 1991) and 65 in Western Australia. It appears to richer than the East African fauna (22 species in Sheppard, 1987), but that situation possibly only reflects the general lack of information on the East African coral fauna.

A REVISION OF THE HARD CORAL FAMILY PORITIDAE Gray, 1842 (Scleractinia: Fungiina) IN SOUTH EAST AFRICA

Abstract

This review presents all 12 species in the genera Porites, Alveopora and Goniopora presently known to occur on the South-East African coast (i.e. the African coast south of the Tropic of Capricorn) and at the atoll Bassas da India in the Mozambique channel. All recorded species are of wide Indo-Pacific distribution. The Mozambiquan fauna was richer than the South African fauna (14 species versus 9 species). Most species are of wide Indo-Pacific distribution, with only one apparently endemic species (Goniopora crassa Crossland). Laboratory and field characteristica are discussed in detail.

Introduction

The Poritidae is the third important family, which is treated in greater detail in this thesis. Members of this family are common all across the Indo-Pacific and are amongst the most important frame-builders. This family is particularly interesting for their capability of commonly building enormous colonies, which may attain several metres in diameter. They mostly dwel on leeward, shallow reef environments (Sheppard & Sheppard, 1991). As such environments are not found in South Africa, but only from Inhaca Island northwards, it can be deduced that poritids will play a more important role in Mozambique than in South Africa. Nevertheless they are common in all South East African reef coral communities and therefore merit special attention.

Material & Methods

Collecting sites were the same as for the material used in Part I, Chapters 2 and 5.

FAMILY PORITIDAE Gray, 1842

Within this important family there are three large genera, Porites, Goniopora and Alveopora, all of which are found in South-East Africa, and one small, monospecific genus, Stylaraea, which occurs in the Western Indian Ocean (Veron & Pichon, 1982), but has not yet been recorded on the Eastern African coast. The family is characterized by a massive growth form and small corallites. The colonies can attain very large sizes of several metres diameter, which makes them, especially the genus Porites, very important frame-builders in almost every coral reef area of the world.

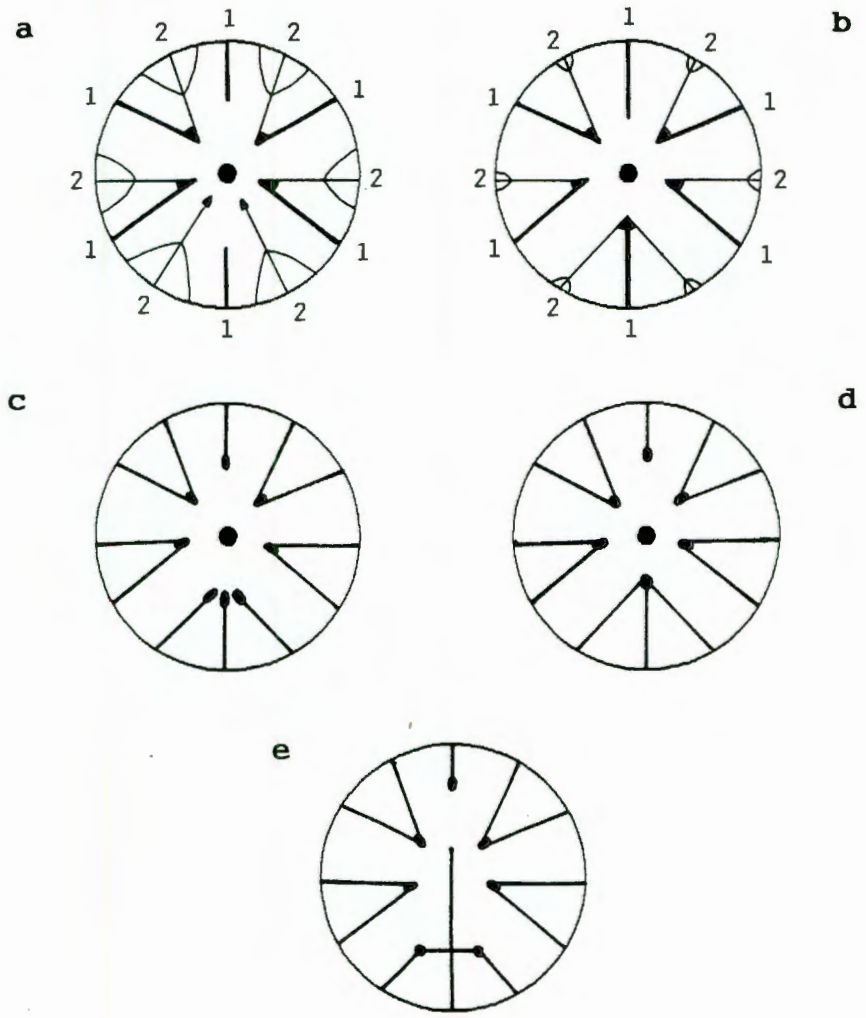


Fig. 1: Diagrams of the patterns of septal arrangement in Goniopora (a) and Porites (b), numbers indicate the orders of the septal cycles. a & b showing how the poritid pattern can be derived from the gonioporoid pattern (after Bernard, 1905 in Veron & Pichon, 1982). c, d & e showing variations in the pattern of septal fusion in Porites as mentioned in the text.

Various stages of reduction of the sceleton occur, reaching a climax in Alveopora, which has a highly reduced sceleton, but nevertheless can form large colonies.

Genus Porites Link, 1807

Generic Synonymy

Porites Link, 1807

Neoporites Duchassaing & Michelotti, 1860

Cosmoporites Duchassaing & Michelotti, 1860

Napopora Quelch, 1886

Porites is one of the most important genera on Indo-Pacific coral reefs. The growth form is typically massive, although three species with nodular to branching growth form are found in our area. This genus is characterized by the distinct pattern of septal arrangement: a short dorsal directive septum, the ventral directive septum and two lateral septa forming a ventral triplet, which may be fused or not, and lateral septa which are mostly fused in pairs. The variations in this pattern are species specific (Fig. 1).

PORITES LUTEA Edwards & Haime, 1860

(Plate 1a)

Synonymy

Porites lutea Edwards & Haime, 1860; Klunzinger (1879); Ortmann (1888); Vaughan (1918); Matthai (1932); Hoffmeister (1925); Wells (1954); Scheer & Pillai (1974); Pillai & Scheer (1976); Scheer & Pillai (1983); Veron & Pichon (1982); Veron (1986); Sheppard (1987); Sheppard & Sheppard (1991).

Porites arenosa Quelch, 1888; Crossland, 1948.

Material examined

3 specimens from Inhaca Island, Mozambique (ORI/BIIC5(1), ORI/BIIC5(5) from Pta. Torres, ORI/BIIC5(5) from Saco da Inhaca); 1 specimen from Bassas da India (ORI/BdI/Por2(1)); 1 specimen from Two-Mile Reef, Central Reef Complex, RSA (ORI/S2/1991-11-17).

Corallum

Massive, round to hillocky in parts (especially in larger colonies).

Corallites

Crowded, polygonal, diameter around 1 mm; distance between adjacent corallites less than 1 whole corallite diameter.

Septa

Ventral triplet fused to give a "trident shape" (Veron & Pichon, 1982); 5 large pali, the one of the dorsal directum septum very small; ventral triplet has usually only one palus; if more than one palus present, then the palus on middle directive septum usually larger than the ones on the lateral directives; pali are fused to the columella by synapticulae (radii); lower synapticular ring (palar ring) is complete, outer synapticular ring is incomplete; distal of the outer synapticular ring septa often become bifurcate ore wedge-shaped; only one denticle, which is close to the wall, in each septum.

Columella

Small, but mostly present, although absent in some corallites.

Thecae

Thin, with a row of spicules on thecal upper edge in some specimens; where the theca is wide, it takes a spongy appearance.

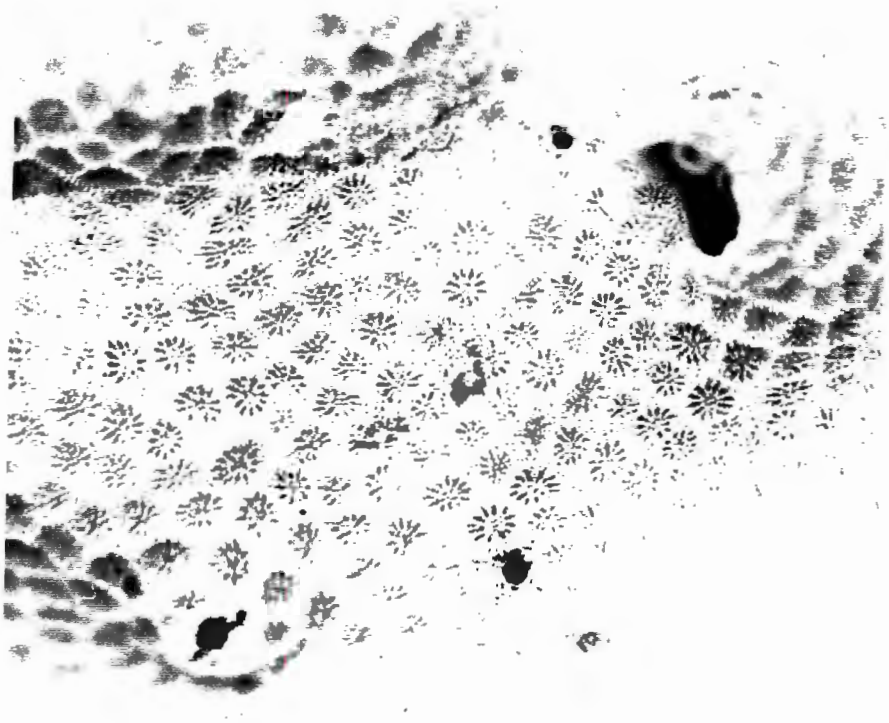


Plate 1a: Porites lutea, Inhaca Island, Mozambique, x3

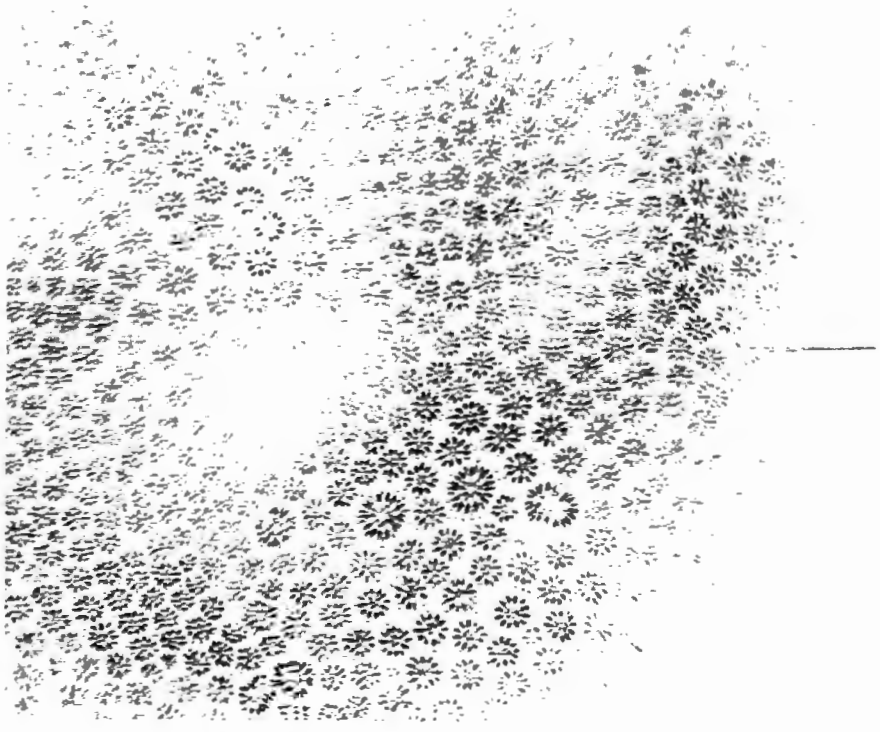


Plate 1b: Porites cf. australiensis, Bassas da India, x2

Observations

P. lutea is a distinctive species due to the unique pattern of fusion in the ventral triplet, which is "trident-shaped" (Veron & Pichon, 1982). The columella is smaller than in P. australiensis and often looks like a palus; it is sometimes compressed in the orientation of the directive septa.

PORITES cf. AUSTRALIENSIS Vaughan, 1918

(Plate 1b)

Synonymy

Porites australiensis Vaughan, 1918; Matthai (1923); Yabe & Sugiyama (1935); Crossland (1952); Wells (1954); Veron & Pichon (1982); Veron (1986); Sheppard (1987).

Material examined

1 specimen from Inhaca Island, Mozambique (ORI/BIIC5(4) from Pta. Torres); 2 specimens from Bassas da India (ORI/BdI/Porl(1), ORI/BdI/Porl(2)).

Corallum

Massive, hemispherical to spherical.

Corallites

Polygonal, crowded; diameter 1-1.5 mm; distance between adjacent calices never more than 1/4 calyx radius.

Septa

Ventral triplet free, only occasionally fused; 8 pali; often the palus on the dorsal directive septum is the smallest; Pali of the lateral septa are bigger than those of the directive septa; the Pali on the ventral directive septa are approximately of the same size; 1 or 2 denticles on the septa, which are lower than the

pali; lower synapticular ring complete, outer synapticular ring incomplete; radii linking septa to columella (not visible on ORI/BIIC5(4)).

Columella

Present, well developed, often compressed in direction of directive septa.

Thecae

Thin, with three rows of spicules on the upper edge.

Observations

On ORI/BdI/Porl(1) the fusion of the ventral triplet only occurs on the hillocky parts of the corallum in about 50% of the calices. ORI/BdI/Porl(2) is a more typical corallum with less variation in the degree of fusion of the ventral triplet.

PORITES SOLIDA (Forskal, 1775)

(Plate 2a)

Synonymy

Madrepora solida Forskal, 1775.

Porites solida (Forskal); Klunzinger (1875); Ortmann (1888); Von Marenzeller (1901, 1907); Vaughan (1918); Crossland (1948); Scheer & Pillai (1974); Pillai & Scheer (1976); Veron & Pichon (1982); Scheer & Pillai (1983); Veron (1986); Sheppard (1987); Sheppard & Sheppard (1991).

Material examined

1 specimens from Inhaca Island, Mocambique (ORI/BIIC1(1), Pta. Rasa); 1 specimen from Xai Xai, Mozambique coast (ORI/BIIC1(1)); 4 specimens from Two-Mile Reef, Central Reef Complex, RSA (ORI/S2/1991-11-18, ZMTAU/VII-B-10, ZMTAU/III-B-11, ZMTAU/I-F-4),

1 specimen from Nine-Mile Reef, Central Reef Complex, RSA (ORI/S9/1991-11-19).

Corallum

Massive, undulating surface.

Corallites

Polygonal, crowded, diameter 1.5-2mm, adjacent corallites only separated by the thin wall.

Septa

Ventral triplet free, dorsal directive septum is a bit shorter or as long as lateral septa; septa do not reach the upper edge of the wall but begin approximately 1/4 of the wall height down; septa often divide near the wall and bear 2-3 hirsute denticles, the innermost of which resemble Pali; within the lateral septal pairs, one is often shorter and bends towards the longer one, which bears the palus.

Columella

Weakly developed to absent; laterally compressed in the same orientation as the directive septa.

Thecae

High, acute, bearing echinulate dentations on the upper edge.

Observations:

This species is readily recognized in the field by the usually very high and acute wall. The absence of clearly differentiated pali and the pattern of fusion (or, rather, non-fusion) of the ventral triplet are very typical.

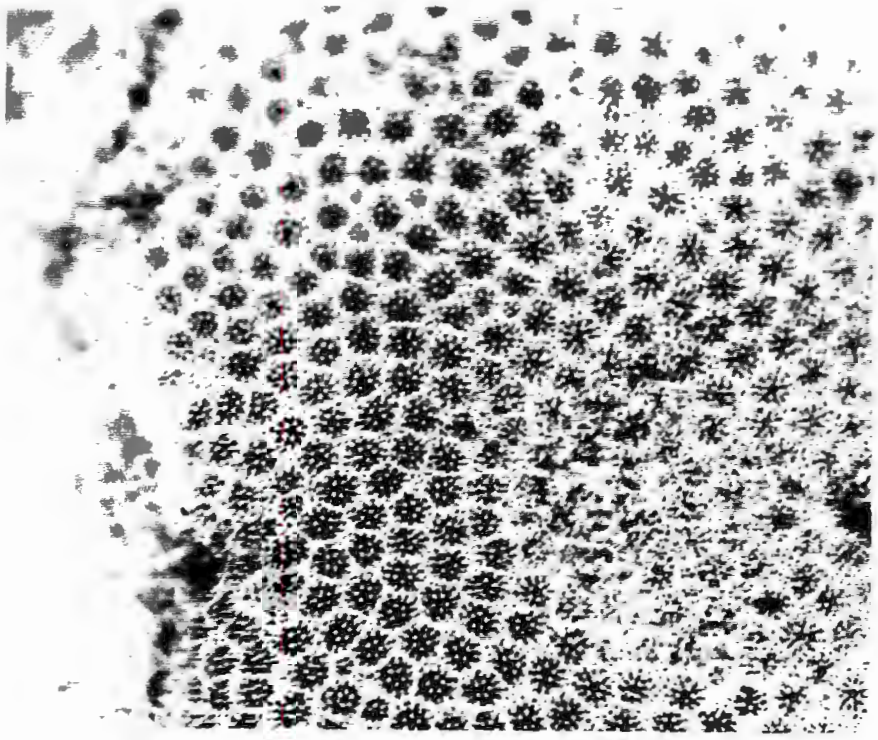


Plate 2a: Porites solida, 2-Mile Reef, South Africa, x2.5

Plate 2b: Porites lichen , Chaka's Rock, South Africa, x1

PORITES LICHEN Dana, 1846

(Plate 2b)

Synonymy

Porites lichen Dana 1846; Bernard (1905); Vaughan (1918); Yabe & Sugiyama (1935); Wells (1954); Veron & Pichon (1982); Veron (1986); Sheppard (1987).

Porites viridis Gardiner, 1898; Bernhard (1905); Vaughan (1918); Boshoff (1981).

Material examined

3 specimens from Inhaca Island, Mozambique (ORI/BIIC3(2), ORI/BIIC3(4) from Pta. Torres, ORI/BIIC3(1) from Baixo 213); 1 specimen from Chaka's Rock, northern Natal coast (ORI/BIIC3(3); 2 specimens from Bassas da India, lagoon (ORI/BdI/1991-8-50, ORI/BdI/1991-8-51).

Corallum

Massive base with nodules, columns and branches.

Corallites

Often in rows (as they are formed by intratentacular budding; extremely variable and heterogeneous, diameter around 0.9 mm. The corallites within the series are separated by much lower and narrower walls than the one separating the series from the rest of the corallum; this pattern is very conspicuous (BdI/1991-8-50).

Septa

Ventral triplet may be free or fused; in some parts of the colonies the septa are only a row of horizontal dentations, where not even the 4 lateral septal pairs are joined; up to eight pali; if ventral triplet is fused, then only one palus present, which is smaller than the other pali.

Columella

Mostly missing; when present, then shorter than the pali.

Observations

This is one of the more common Porites species in South Africa. Underwater it is easily identified by its generally green colouration and the hillocky or branching, very irregular growth form. Also, the linear arrangement of the corallites, especially on hillocky parts is easily recognized.

PORITES NIGRESCENS (Dana, 1846)

(Plate 3a)

Synonymy

Porites nigrescens Dana, 1848; Edwards & Haime (1860); Bernhard (1905); Vaughan (1918); Yabe & Sugiyama (1935); Faure (1977); Boshoff (1981); Veron & Pichon 91982); Veron (1986); Sheppard (1987).

Material examined

1 specimen from Inhaca Island, Mozambique (ORI/BIIC7(1)); 2 specimens from Bassas da India (ORI/BdI/1991-8-33, ORI/BdI/1991-8-60), 1 specimen from 2-mile Reef, Central Reef Complex, RSA (SAM-H-4688).

Corallum

Branching, branches tapering with acute tips; branchlets cylindrical, laterally slightly compressed.

Corallites

Markedly concave with deep central fossa, diameter 1-1.5 mm; polygonal; intercalicular distance less than 1 mm.

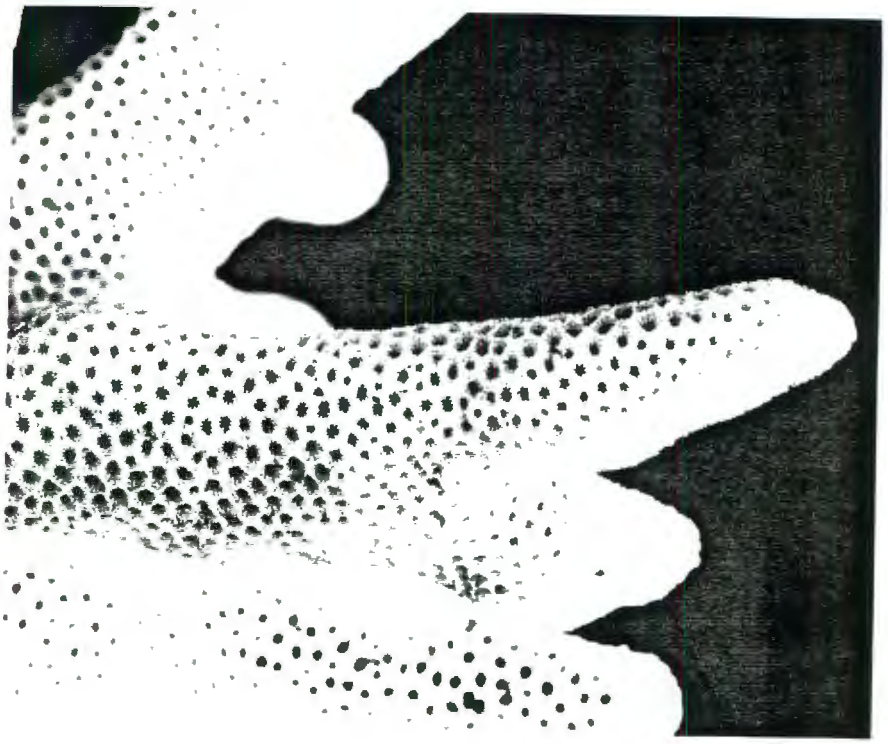


Plate 3a: Porites nigrescens, Bassas da India x1.5

Plate 3b: Porites cylindrica, Bassas da India, x1

Septa

Ventral triplet mostly free, fused only in a few corallites; pali are well developed when the ventral triplet is fused; septa are thick with only one denticle and a palus.

Columella

Not always developed; when present styliform.

Observations:

This is the only truly branching Porites species found on the South East African mainland coast. Soth African specimens exhibit less branching than specimens from Mozambique. Affinities to P. cylindrica are discussed below.

PORITES CYLINDRICA Dana, 1846

(Plate 3b)

Synonymy

Porites cylindrica Dana, 1846; Bernard (1905); Vaughan (1918); Chevalier (1968); Veron & Pichon (1982); Veron (1986); Sheppard (1987).

Porites andrewsi Vaughan, 1918; Hoffmeister (1925); Yabe & Sugiyama (1935); Pillai & Scheer (1973, 1976); Faure (1977).

Material examined:

2 specimens from Bassas da India, Lagoon (ORI/BdI/1991-8-61, ORI/BdI/1991-8-62).

Corallum

Branching with short, stout branches.

Corallites

Much less concave than in P. nigrescens; diameter around 1 mm, crowded, polygonal; distance between corallites can vary between

crowded and less crowded parts of the corallum.

Septa

Ventral triplet fused; pali well developed, smaller on lateral septa than on the directives; dorsal directive septum shorter than the lateral septa; in the ventral triplet a palus may be developed only on the directive septum or, alternatively, only on the two lateral septa with the directive septum devoid of a palus; all septa with two denticles between the pali and the wall.

Columella

Well developed; as tall as the pali.

Theca

Ill defined, no ridges on the wall.

Observations:

Although P. nigrescens and P. cylindrica share a common growth form, they are easily separated. P. nigrescens is characterized by mostly straight, tapering and pointed branches, and markedly concave corallites. In P. cylindrica the branches are usually much less tapering and can be very blunt. The corallum has a very smooth appearance in contrast to the "pitted" appearance of P. nigrescens. The distribution of P. cylindrica does not seem to reach the African mainland as it has only been encountered on Bassas da India.

PORITES COMPRESSA Dana, 1846

Synonymy

Porites compressa Dana 1846.

Material examined

1 specimen from Inhaca Island, Mozambique (ORI/BIIc4(2) from Pta.

Torres).

Corallum

Columnar to branching with blunt ends.

Corallites

Crowded, polygonal, diameter around 1,5 mm, seperated by only a thin theca; strongly concave, which gives a pitted appearance; budding is extratentacular.

Septa

Ventral triplet is free; 8 pali, the one on the the directive septa is smaller than on the lateral septa. 2 denticles on each septum, both smaller than the Pali; lower synapticular ring often present, outer synapticular ring usually absent; some bifurcation of lateral septa before they reach the wall; septa linked to the columella by synapticulae.

Columella

Present, in form of a tooth and smaller than the pali; may be laterally flattened in direction of directive septa.

Thecae

Thin, acute, with a line of dentations on upper margin.

Observations

More material is needed to ascertain the correctness of the identification and the presence of this species in South-East Africa.

PORITES LOBATA Dana, 1846

Synonymy

Porites lobata Dana, 1846. Edwards & Haime (1860); Vaughan (1918); Crossland (1952); Wells (1954); Scheer & Pillai (1974); Veron & Pichon (1982); Veron, 1986; Sheppard (1987); Sheppard & Sheppard (1991).

Material examined

1 specimen from Inhaca Island, Mozambique (ORI/BIIC5(3)).

Corallum

Massive, hemispherical.

Corallites

Crowded, polygonal, diameter 1 to 2 mm; distance between adjacent calices always less than one whole calyx diameter.

Septa

Ventral triplet mostly free, only on hillocky parts is the ventral triplet fused; one palus on each septum and two dentations, which are larger than the palus; Pali of directive septa are smaller than those of lateral septa; septa joined to the columella by radii.

Columella

Present, columnar, smaller than Pali.

Thecae

Up to 1 mm wide, spongy, with a row of denticles on its upper surface.

Observations

More material is needed to ascertain the correctness of the identification and the presence of this species in South East Africa.

Genus Goniopora Blainville, 1830

Generic synonymy (after Veron & Pichon, 1982):

Goniopora de Blainville, 1830; Quoy & Gaimard (1833); Quelch (1886).

Litharaea Edwards & Haime, 1850.

Rhodararea Edwards & Haime, 1849; Quelch (1886).

Tichopora Quelch, 1886.

Goniopora is an easily recognized genus with long, fleshy polyps, which are extended by day. It has the biggest corallites in the family Poritidae, with a very distinctive septal pattern. Septa are basically in three orders, but this situation is not always discernible (Bernard, 1903; Veron & Pichon, 1982). Septal fusion does not follow as fixed a pattern as in the genus Porites.

GONIOPORA DJIBOUTENSIS Vaughan, 1907

(Plate 4a)

Synonymy

Goniopora djiboutensis Vaughan, 1907b; Veron & Pichon, 1982; Veron, 1986; Sheppard (1987); Sheppard & Sheppard (1991).

Material examined

2 specimens from Two-Mile Reef, Central Reef Complex, RSA (ORI/S2/1991-6-9, ORI/S2/1991-6-10), 2 specimens from Inhaca Island, Mozambique (ORI/BIIb1(1), ORI/BIIb1(3) from Pta. Rasa).

Corallum

Massive, cushion shaped, very irregular in outline.

Corallites

Large and deep, diameter 3-5 mm, very irregular, polygonal, only on rounded parts of the corallum are there some round corallites (S2/1991-6-9).

Septa

Very regular and size classes easily distinguishable, gonioporoid pattern of fusion mostly not apparent; with well developed dentations and paliform lobes on the biggest septa, these are not developed in all corallites; septal sides slightly granulated; exsert.

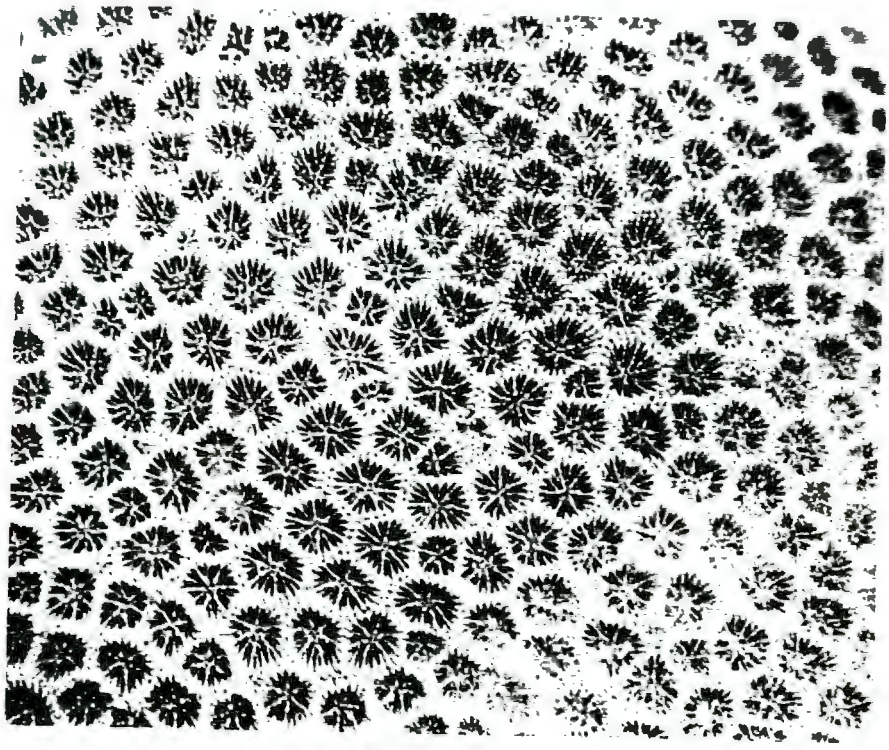


Plate 4a: Goniopora djiboutensis, 2-Mile Reef, South Africa, x1.5

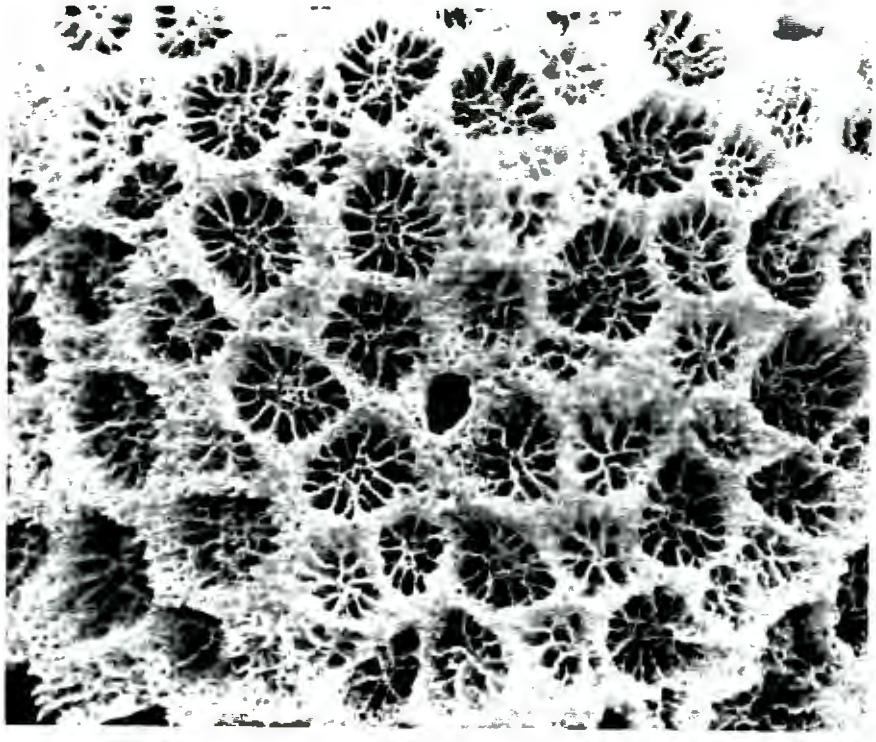


Plate 4b: Goniopora stokesi, Inhaca Island, Mozambique, x2.5

Columella

From large and very apparent to only moderately developed; always fused to the inner end of the septa.

Thecae

Diameter mostly around 1 mm, compact.

Observations:

Goniopora djiboutensis is common in South Africa and is easily recognized by the large polyps of usually brown colour with a protruding oral field. The skeleton is easily identified because the large corallites have better-developed columellae than G. stokesi.

GONIOPORA STOKESI Edwards & Haime, 1851

(Plate 4b)

Synonymy

Goniopora stokesi Edwards & Haime, 1851; Edwards & Haime (1860); Ortmann (1888); Scheer & Pillai (1974); Veron & Pichon (1982); Veron (1986); Sheppard (1987); Sheppard & Sheppard (1991).

Material examined

1 specimen from Inhaca Island, Mozambique (ORI/BIIb1(2) from Pta. Torres).

Corallum

Massive, sperical; surface with small irregular humps.

Corallites

Polygonal and very irregular; diameter 2-4 mm, depth mostly from 3-45 mm; numerous young corallites produced by extratentacular budding are visible.

Septa

Gonioporoid pattern of fusion well developed in all corallites; septa are thin and begin about one millimeter from the edge of the calyx wall, dentations are fine although in some corallites very well developed; no paliform lobes.

Columella

Well developed though set deep inside the calyx; fused to all septa.

Theca

Thin, one half to one mm diameter; perforate in the upper part.

Observations

This species seems to have its southern limits in Mozambique as it has not yet been found in South Africa. It is close to G. djiboutensis, but lack the paliform lobes and the well developed columella.

GONIOPORA SOMALIENSIS Vaughan, 1907

(Plate 5a)

Synonymy

Goniopora somaliensis Vaughan, 1907b; Veron & Pichon (1982); Veron (1986); Sheppard (1987); Sheppard & Sheppard (1991).

Material examined

4 specimens from Two-Mile Reef, Central Reef Complex, RSA (ZMTAU/I-F-7, ZMTAU/II-D-3, ZMTAU/P-3-4; ORI/S2/1991-6-11).

Corallum

Thin to submassive plates often with laminar edges.

Corallites

Diameter 1.8-3 mm, very shallow, polygonal; intercalicular distance 0.8-1 mm.

Septa

Long first order septa, which reach the columella and bear very prominent pali; second order septa are short and descend abruptly into into the calyx; they are mostly free, but a gonioporoid pattern of fusion can sometimes be observed; pali reach to the same height as the theca and bear elaborate spines; they are often laterally flattened and fused to the columella; all septa bear dentations and have granulated sides.

Columella

Generally well developed, either in form of twisted trabeculae or in form of a solid rod, which may be as high as the pali and laterally flattened.

Thecae

Relatively thick compared to calyx diameter, made up of septa and linking synapticles; it therefore appears very porous.

Observations

Goniopora somaliensis is common on South African reefs. It is easily recognized both in life and as bleached skeleton by the much smaller polyps and corallites, which separate it from the other common species, G. djiboutensis.

The identity of specimen ZMTAU/IV-A-5 is unclear. It is a very small specimen from Two-Mile Reef, RSA, which strongly resembles Goniopora tenuidens. More material would be needed to confirm the presence of this species, which has not yet been recorded as far west as the African coast.

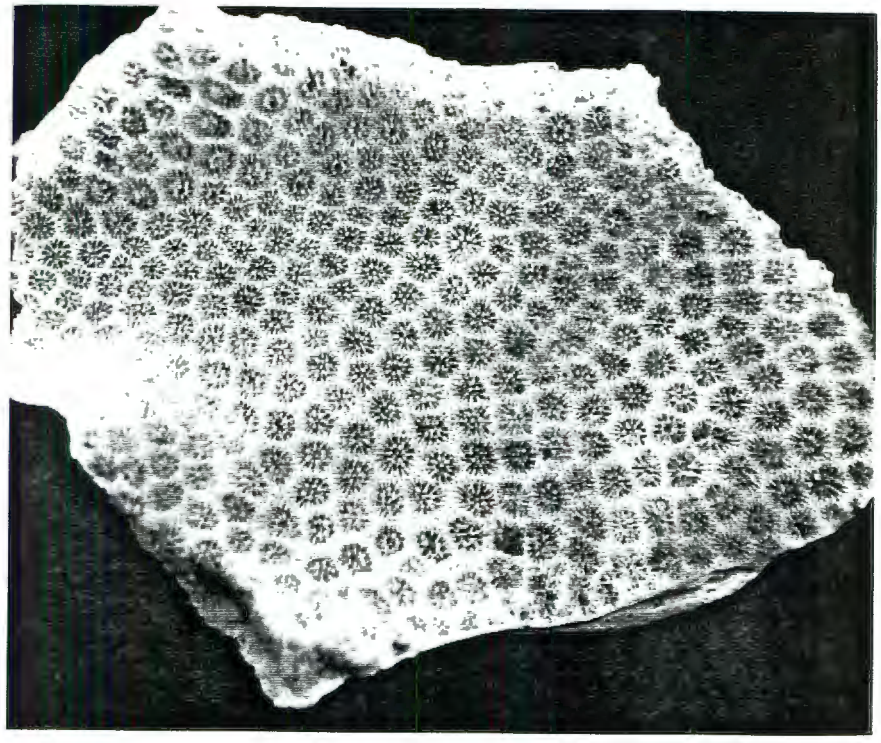


Plate 5a: Goniopora somaliensis, 2-Mile Reef, South Africa, x1.5

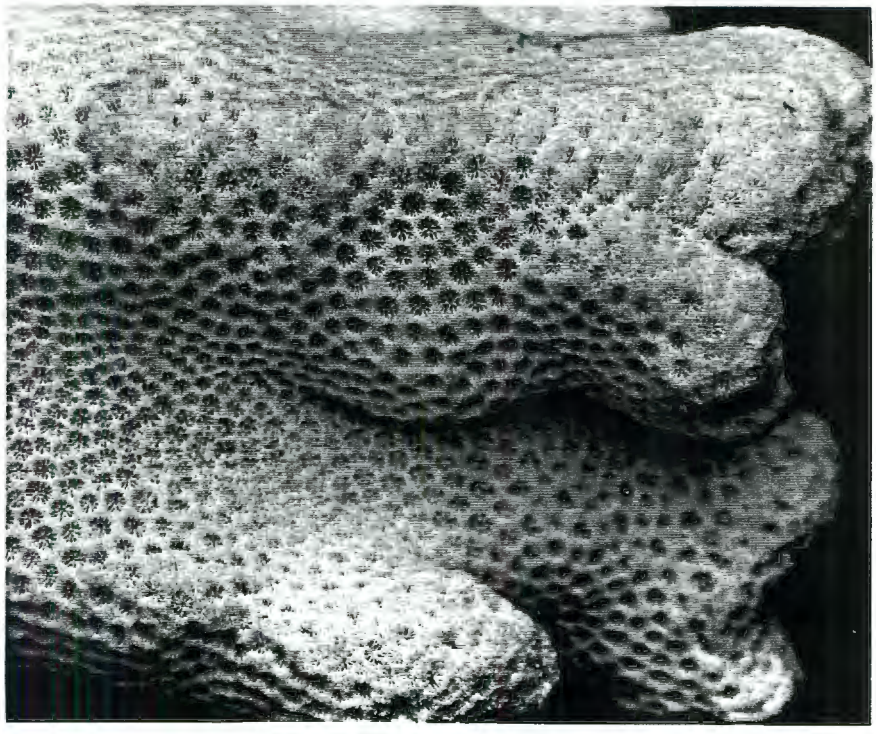


Plate 5b: Goniopora lobata, Inhaca Island, Mozambique, x2.5

GONIOPORA LOBATA Edwards & Haime, 1860

(Plate 5b)

Synonymy

Goniopora lobata Edwards & Haime, 1860; Bernard (1903); Vaughan (1907); Crossland (1948, 1952); Wells (1955); Veron & Pichon (1982); Veron (1986); Sheppard (1987).

Material examined

1 specimen from Inhaca Island, Mozambique (ORI/BIIC2(2) from Baixo 213).

Corallum

Massive, columnar.

Corallites

Polygonal and shallow, diameter 1.5-3 mm.

Septa

Mostly in three size classes, gonioporoid pattern of fusion generally well developed; first order septa may bear large spines, which appear like pali, these can be laterally flattened; all septa with spines of various development; sides granulated; only the two longest septal cycles fused to the columella.

Columella

Generally well developed in most calices, consisting of fused trabeculae and synapticulae.

Thecae

Very porous.

Observations

This species has not been found south of Inhaca Island, where it

appears to be uncommon. It is the only local Goniopora with a columnar growth form.

GONIOPORA CRASSA Crossland, 1948

Judging from Crossland's description this seems to be a valid species. No specimen could, however, be found in the present collection.

G. crassa differs from all other local Goniopora by the extremely thick corallite walls (Crossland, 1948).

Genus Alveopora Blainville, 1830

This genus has had a somewhat turbulent taxonomic history, being placed within and without the Poritidae by several authors (reviewed by Veron & Pichon, 1982). The skeleton is typically very reduced consisting only of loosely intertwined and joined trabeculae. This adds considerably to the difficulties when working on this genus.

ALVEOPORA SPONGIOSA Dana, 1846

(Plate 6a)

Synonymy

Alveopora spongiosa Dana, 1846; Veron & Pichon (1982); Sheppard (1987); Sheppard & Sheppard (1991).

Material examined

2 specimen from Two-Mile Reef, Central Reef Complex, RSA (ORI/S2/2-12-13/8, ZMTAU/IV-F-24); 2 specimens from Four-Mile Reef, Central Reef Complex, RSA (ORI/S5/1991-11-15, ORI/S5/1991-

11-16); 1 specimen from Inhaca Island, Mozambique (ORI/BIIa2(1) from Saco da Inhaca).

Corallum

Massive (as far as the term applies in a species with such a fragile skeleton), hemispherical; ORI/BIIa2(1) is only a small nodule which however shows the same growth tendencies as ORI/S2/2-12-13/8.

Corallites

Polygonal, crowded, diameter 1.5-2 mm.

Septa

Very reduced, only present in form of tapering spines up to 1/4R; these spines may fuse in the centre and then strech across the entire calyx. Spines originate at various depths in the calyx; if more than one spine is present, the spines are arranged in rows; no complete cycles discernible.

Columella

Missing.

Theca

Mostly hexagonal or heptagonal; each side is made up of two to three trabecular palisades connected by synapticulae at more or less regular intervals.

Observations

This species is not uncommon on deep reefs in South Africa, where it can form colonies of up to 2m diameter. It is easily distinguished from A. allingi by its completely different growth form and its smaller corallites. The living animal has shorter polyps than in the previous species.

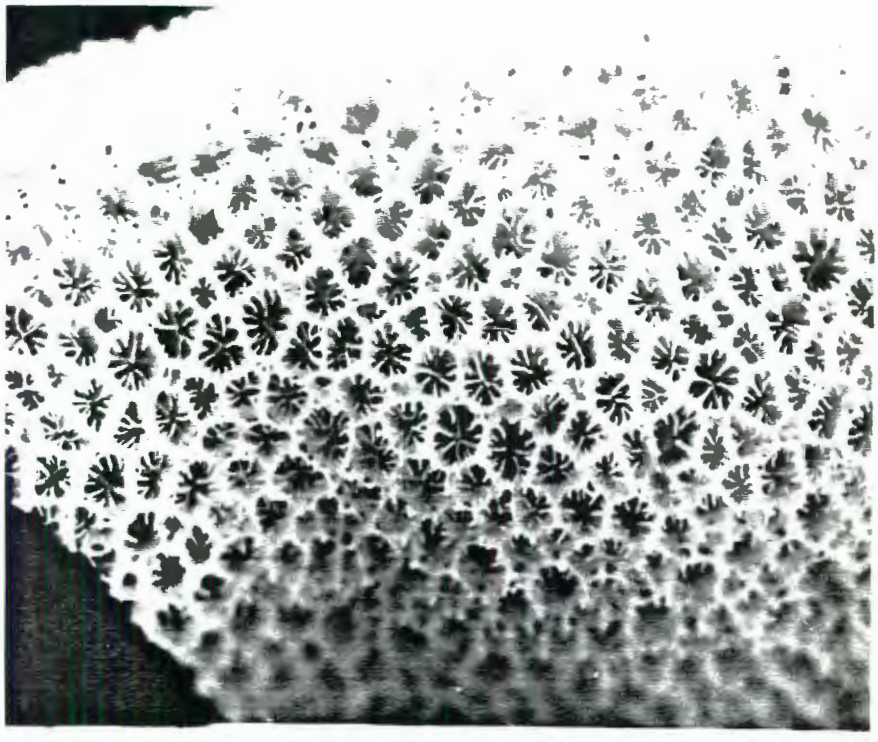


Plate 6a: Alveopora spongiosa, 4-Mile Reef, South Africa, x2

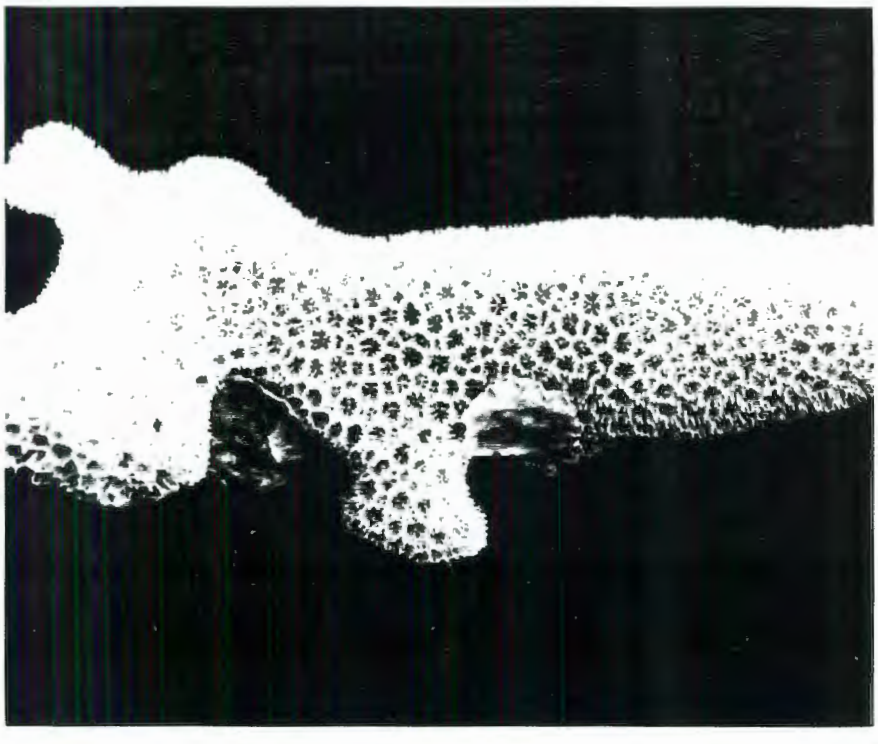


Plate 6b: Alveopora allingi, 4-Mile Reef, South Africa, x0.7

ALVEOPORA ALLINGI Hoffmeister, 1925

(Plate 6b)

Synonymy

Alveopora allingi Hoffmeister, 1925; Wells (1954); Pillai & Scheer (1976); Veron & Pichon (1982); Veron (1986); Sheppard (1987); Sheppard & Sheppard (1991).

Material examined

6 specimens from Kosi Bay, Northern Reef Complex, RSA (ORI/KB/1991-9-1, ORI/KB/1991-9-17, ORI/KB/1991-9-39, ORI/KB/1991-9-40, ORI/KB/1991-9-41, ORI/KB/1991-9-56), 1 specimen from Four-Mile Reef, Central Reef Complex, RSA (ORI/S5/1991-11-14).

Corallum

Short, blunt and very irregular branches arising from an incrusting to submassive base.

Corallites

Polygonal, crowded, of very irregular size and shape, diameters vary from 1-4 mm, often in adjacent corallites; corallites tend to get smaller towards the tips of branches.

Septa

Development varies from no septa at all (ORI/KB/1991-9-1) to two well developed cycles; in all cases septa consist only of spines which often fuse with the columella; opposite spines may fuse and then span across the calyx; depending on the development, septa consist of a more or less accurate vertical row of spines or only of one or a few individual spines per septum.

Columella

May be completely absent or well developed; in individual corallites only the columellae, but not the septa can be present

(ORI/KB/1991-9-1); when present, columellae usually fuse with the septal spines.

Thecae

In all specimens very porous, consisting only of vertical trabecular rods interconnected by synapticulae.

Observations

This is the most common South African species of Alveopora. It is mostly found on flat, deep bottom at depths around 20m. Although this species is very polymorphic, both in growth form and the development of its skeleton, it is readily recognized, as it is the only species in South Africa which forms short branches.

Discussion

The Poritidae are, similar to the genus Acropora, very good indicators of narrowly defined habitats on the reefs. They are, over much of their distributional range, usually indicators of back-reefs or leeward reef-slopes (Sheppard & Sheppard, 1991). It is therefore not surprising, that the poritid fauna of Mozambique and Bassas da India are much richer than the South African fauna. In Mozambique 14 species were found, versus 9 species in South Africa. On Bassas da India one further species (P. cylindrica), which has not yet been recorded from the African mainland coast, was found. It is believed that the lower species richness in South Africa reflects the lower diversity of habitats, which do not provide tha same amount of ecological niches as the reefs in Mozambique (see Part II). Porites are regularly found in tidal

pools as far as southern Natal and are also present on Aliwal Shoal (at least one species, P. lichen). Within South Africa Porites usually never grows to the same size as in Mozambique or Bassas da India. The biggest colonies encountered were Porites lutea in the Central Reef Complex, northern Natal, with a diameter of two metres. The growth form of the branching P. nigrescens in South Africa, where it is rare, is always very stunted and indicates sub-optimal habitat. The present study shows clearly, that South Africa is already outside the central distributional range of this family.

DISCUSSION OF PART I

Discussion

The taxonomic reviews in the previous chapters provide the first detailed account of the hitherto relatively unknown coral fauna of South Africa and the scantily known fauna of Mozambique. It is now possible to consider these local faunas in relation to larger Indo-Pacific biogeographical patterns.

The biogeography of Indian Ocean corals has been the subject of intensive research and speculation (Rosen, 1988; Jokiel & Martinelli, 1992). Unfortunately, large gaps in our knowledge concerning the coral fauna of Eastern Africa remain. In the light of new biogeographical theories (Jokiel & Martinelli, 1992) it is, however, very important to have information about this area. The present revisions, together with the list given in Wijsman-Best et al. (1980) for Mozambique and the Seychelles, allow us to draw an accurate picture of the coral fauna of the southern part of this region.

Jokiel & Martinelli (1992) postulated in their "vortex model of coral reef biogeography" that coral distribution is driven by major ocean currents. They postulated a much higher westward than eastward transport of coral larvae, due to oceanic current patterns. Starting from a hypothetical uniform distribution of species accross the ocean, diversity centres on the western boundaries of the oceans should develop due to larval transport by currents and allopatric speciation. They thus explain the diversity centre of the Pacific in the Indo-Australian region and the diversity centre of the Atlantic in the Caribbean. It is also postulated that faunal attenuation along the eastern boundaries can be explained by this mechanism. According to this theory, East

Africa should be the diversity centre of the Indian Ocean, while faunal attenuation should be observed in Western Australia. This, however, is not the case. On the contrary, more genera and species have so far been recorded in western Australia than in East Africa (Veron, 1985; Sheppard, 1987; Veron & Marsh, 1988). Does this mean that Jokiel & Martinelli's (1992) hypothesis is wrong? For two reasons this is not the case. There exists a diversity peak in the northern Indian Ocean in the Arabian region (Sheppard, 1987; Sheppard & Sheppard, 1991), although it is only marginally richer than the eastern boundary. In the southern Indian Ocean the situation still needs to be clarified. While tropical East Africa actually is the western boundary to the southern oceanic gyre, subtropical South East Africa is not. South Africa and Mozambique lie within a distinct current pattern, influenced by the gyral system in the Mozambique channel and the Agulhas current, but they are not directly influenced by the larger oceanic gyral system (Fig.1). The southern Indian Ocean diversity centre should theoretically therefore be located on the Eastern Madagascan coast and the tropical East African Coast, but the coral fauna of these areas is poorly known. The South East African coral fauna theoretically would be recruited by larvae transported south along the African Coast. As numerous big rivers, like the Zambesi, enter the sea in this area and most of the South East African coastline is sandy and unstable, it would appear plausible that this coral fauna could be much poorer than its tropical counterpart. Figure 1 shows however, that this apparently is not the case. A marked decline in diversity occurs only between southern Mozambique and northern Natal, while species richness seems to be uniform all

along the east African coast. This situation is similar to that observed in the Red Sea, where high latitude reefs are richer, or at least as rich, as their tropical counterparts (Sheppard, 1987; Sheppard & Sheppard, 1991). There is, however, a possibility that the given distribution of diversity reflects more a distribution of "publication richness" than of actual faunal richness as the areas, which have received most attention, are those with the highest recorded diversity. On that score it is difficult to imagine a tropical area like East Africa to be poorer in species than a marginal, subtropical area such as southern Mozambique. It is therefore not possible to properly evaluate the validity of Jokiel & Martinelli's (1992) hypothesis for the southern Indian Ocean due to the large gaps in our knowledge about the tropical East African coral fauna.

The Eastern African, and to a lesser extent also the South East African, coral fauna has quite a strong component of endemic genera and species (Ancmastrea, Horastrea, Erythrastrea, Gyrosmilia, Astraeosmilia). In the previous chapters, 4 species of Acropora were described, which also seem to be endemic to this region. This fits in well with current biogeographic hypotheses. Rosen (1984) postulates neogene speciation as due to "glacio-eustatic disruption of existing...population patterns". Jokiel & Martinelli (1992) enhanced this scenario by adding current patterns and deep-water areas as barriers. Using Hawaii as an example, they argued that for speciation a relatively small stock of species is needed, which is more or less isolated from the diversity center. Within the subregion gene flow would exist but

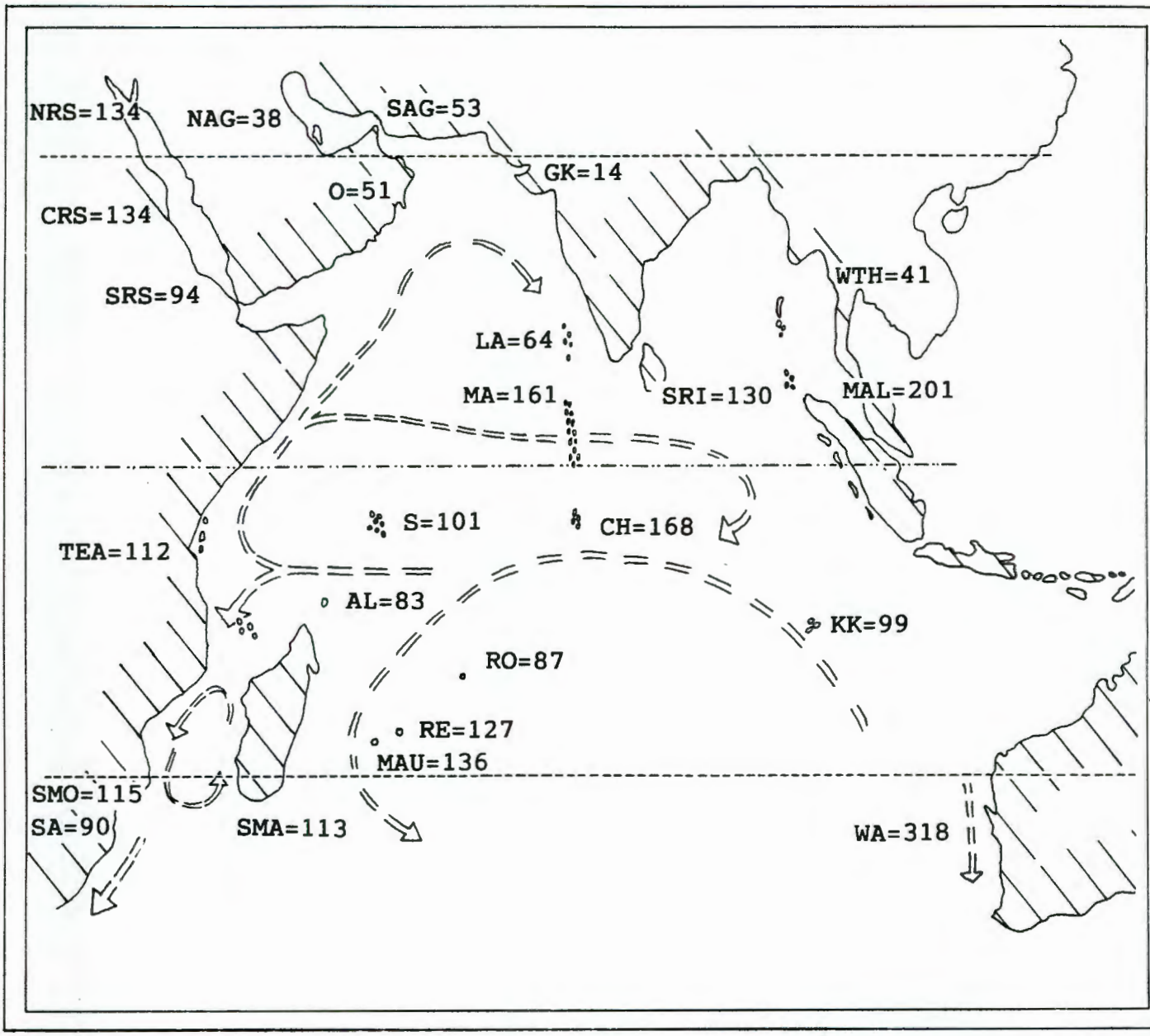


Fig. 1: Distribution of hermatypic coral species richness across the Indian Ocean. Numbers are taken from Sheppard (1987), except for Kokos-Keeling (Veron, 1990), Western Australia (Veron & Marsh, 1988), South Africa and Mozambique (this study). Major current patterns, as used by the Vortex Theory (Jokiel & Martinelli, 1992) to explain coral species richness distribution are indicated (modified after Branch & Branch, 1983; de Freitas, 1984). AL=Aldabra, CH=Chagos, CRS=Central Red Sea, GK=Gulf of Kutch, KK=Kokos-Keeling, LA=Lakkadives, MA=Maldives, MAL=Malakka Peninsula, MAU=Mauritius, NAG=Northern Arabian Gulf, NRS=Northern Red Sea, RE=Reunion, RO=Rodrigues, S=Seychelles, SA=South Africa, SAG=Southern Arabian Gulf, SMA=Southern Madagascar, SMO=Southern Mozambique, SRI=Sri Lanka, SRS=Southern Red Sea, TEA=Tropical East Africa, WA=Western Australia, WTH=Western Thailand.

little or no fresh imput would be provided by the diversity center. A similar situation appears to exist in the South East African region, where the reefs are seperated from the (postulated) East African center of diversity by the Zambezi mouth and almost 1000km without any significant coral reef areas. This relative isolation may have been enough to allow speciation, especially within such a plastic genus as Acropora.

It is also within the genus Acropora that the most drastic decline in species richness is observed between Mozambique and South Africa. This may largely be due to the restricted amount of suitable habitat available on South African reefs (see Part II, Chapter 1).

Conclusion

The hitherto largely unknown hermatypic coral fauna of South Africa and the little-known coral fauna of Mozambique were found to be very rich with 90 and 115 species respectively. The drop in species richness between these two areas is most probably due to reduction in habitat availability in South Africa (see Part II, Chapter 1). Most of the occurring species are of wide Indo-Pacific distribution, although a small endemic component is present.

A CHECKLIST OF THE HERMATYPIC SCLERACTINIA OF SOUTH EAST AFRICA

Abstract

A complete checklist of hermatypic coral species known to occur in South Africa and southern Mozambique is given. This list makes obsolete Boshoff's (1981) list, which is fraught with taxonomic errors and misidentifications.

Family Species	South Africa	Mozambique
Astrocoeniidae		
Stylocoeniella guentheri	-	X
Pocilloporidae		
Seriatopora hystrix	-	X
Seriatopora caliendrum	?	X
Stylophora pistillata	X	X
Pocillopora damicornis	-	X
Pocillopora verrucosa	X	X
Pocillopora eydouxi	X	?
Acroporidae		
Montipora venosa	X	X
Montipora spongodes	X	X
Montipora aequituberculata	X	X
Montipora tuberculosa	X	X
Montipora monasteriata	X	X
Montipora verrucosa	X	X
Montipora danae	X	X
Acropora palifera	X	X
Acropora humilis	X	X
Acropora gemmifera	-	X
Acropora monticulosa	-	X
Acropora clathrata	X	X
Acropora nasuta	X	X
Acropora valida	-	X
Acropora secale	-	X
Acropora tenuis	X	X

Acropora striata	-	X
Acropora millepora	X	X
Acropora formosa	-	X
Acropora microphthalma	-	X
Acropora horrida	X	?
Acropora austera	X	X
Acropora aculeus	X	X
Acropora latistella	X	X
Acropora nana	-	X
Acropora danai	X	X
Acropora anthocercis	X	X
Acropora hyacinthus	X	X
Acropora cytherea	-	X
Acropora florida	X	X
Astraeopora myriophthalma	X	X
Poritidae		
Porites lichen	X	X
Porites solida	X	X
Porites lutea	X	X
Porites nigrescens	X	X
Porites cylindrica	X	X
Porites lobata	-	X
Porites compressa	-	X
Goniopora djiboutensis	X	X
Goniopora somaliensis	X	?
Goniopora crassa	X	X
Goniopora stokesi	-	X
Goniopora lobata	-	X

Alveopora allingi	X	X
Alveopora spongiosa	X	X
Siderastreidae		
Psammocora haimeana	X	X
Anomastrea irregularis	X	X
Coscinarea monile	X	X
Coscinarea columna	X	X
Horastrea indica	X	X
Agariciidae		
Pavona clavus	X	X
Pavona decussata	-	X
Pavona minuta	X	X
Leptoseris explanata	X	X
Gardineroseris planulata	X	X
Coeloseris mayeri	X	X
Pachyseris speciosa	X	X
Fungiidae		
Cycloseris costulata	X	X
Cycloseris cyclolites	X	X
Cycloseris marginata	X	X
Diaseris distorta	X	-
Fungia (Pleuractis) scutaria	-	X
Fungia (Verillofungia) concinna	_	X
Fungia (Danafungia) scruposa	-	X
Herpolitha limax	-	X
Polyphyllia talpina	-	X
Podabacia crustacea	X	X

Oculinidae		
Galaxea fascicularis	X	X
Galaxea astreata	-	X
Pectiniidae		
Echinophyllia aspera	X	X
Oxypora lacera	-	X
Mussidae		
Blastomussa merleti	X	-
Acanthastrea ecinata	X	X
Acanthastrea simplex	X	X
Symphyllia valenciennesi	X	-
Lobophyllia corymbosa	-	X
Lobophyllia hemprichi	-	X
Scolymia cf. vitiensis	X	-
Merulinidae		
Hydnophora exesa	X	X
Hydnophora microconos	X	X
Merulina ampliata	-	X
Faviidae		
Favia favus	X	X
Favia pallida	X	X
Favia speciosa	X	X
Favia laxa	X	X
Favia matthai	X	X
Favia rotumana	X	X
Favia stelligera	X	X
Favites abdita	X	X
Favites complanata	X	X

Favites peresi	X	X
Favites flexuosa	X	X
Favites halicora	X	X
Goniastrea pectinata	X	X
Goniastrea retiformis	X	X
Goniastrea edwardsi	X	X
Platygyra daedalea	X	X
Leptoria phrygia	-	X
Oulophyllia cripsa	X	X
Leptastrea purpurea	X	X
Leptastrea bottae	-	X
Cyphastrea chalcidcum	X	X
Echinopora gemmacea	X	X
Echinopora lamellosa	-	X
Echinopora hirsutissima	X	X
Montastrea annuligera	X	X
Montastrea curta	-	X
Plesiastrea versipora	X	X
Caryophylliidae		
Gyrosmilia interrupta	X	X
Dendrophylliidae		
Turbinaria mesenterina	X	X
Tubastraea micranthus	X	X

L I T E R A T U R E

C I T E D

I N

P A R T

O N E

Alloiteau, J. 1957. Contribution a la systematique des Madreporaires fossiles. CNRS, Paris, 1-461.

Antonius, A., Scheer, G. & Bouchon C. 1990. Corals of the Eastern Red Sea. Atoll Research Bulletin 334: 1-22.

Audouin, V. 1826. Explication sommaire des planches des polypes. In: Description de l'Egypte. Savigny, J.C. 1: 225-244, pl.14.

Basset-Smith, P.W. 1890. Report on the stony corals from the Lizard and Macclesfield Banks, China Sea. Ann. Mag. Nat.Hist. (6)6: 353-374.

Bernard, H.M. 1879. The genus Montipora. The genus Anacropora Cat. Madreporarian Corals Br. Mus. (Nat. Hist.) 3: 1-192, pl.1-34.

Bernard, H.M. 1900. Marine fauna of Christmas Island (Indian Ocean). Proc. Zool. Soc. Lond.: 115-141.

Bernard, H.M. 1905. The family Poritidae II. The genus Porites, Part 1. Porites of the Indo-Pacific region. Cat. Madreporarian Corals Br. Mus. (Nat. Hist.) 5: 1-303, pl.1-35.

Bernard, H.M. 1906. The family Poritidae II. The genus Porites, Part 2. Porites of the Atlantik and West-Indies with the European fossil forms. The genus Goniopora, a supplement to Vol.4. Cat. Madreporarian Corals Br. Mus. (Nat. Hist.) 6: 1-173, pl.1-17.

Blainville, H.M. de. 1830. Zoophytes in "Dictionnaire des Sciences naturelles", Paris, 60: 310-358.

Blainville, H.M. de. 1834. Manuel d'Actinologie ou de Zoophytologie. Paris, 2 Vol. VIII: 1-694, pls. 1-101.

Boschma, H. 1923. The Madreporaria of the Siboga expedition. IV. Fungia patella. Siboga-Expeditie 16d: 129-148, pl.9-10.

Boshoff, P. 1980. The corals of Maputaland. in: Bruton, M.N. & Cooper, K.H. (eds): Studies on the ecology of Maputaland. Rhodes Univ. and Wildlife Soc. Natal: 11-113.

Boshoff, P. 1981. An annotated checklist of Southern African Scleractinia. Investigational Report Oceanographic Research Institute, Durban, 1-44.

Branch, G.M. & Branch, M. 1983. The living shores of Southern Africa. Struik. Cape Town.

Brook, G. 1891. Description of new species of Madrepora in the collections of the British Museum. Ann. Mag. Nat. Hist. (6)8: 458-471.

Brook, G. 1892. Preliminary descriptions of new species of Madrepora in the collections of the British Museum. Part II. Ann. Mag. Nat. Hist. (6)10: 451-465.

Brook, G. 1893. The genus Madrepora. Cat. Madreporarian corals Br. Mus. (Nat. Hist.) 1: 1-212, pl.1-35.

Brueggemann, F. 1879a. Corals in zoology of Rodriguez. Phil. Trans. R. Soc. Lond., B. Biol. Sci. 168: 569-579.

Brueggemann, F. 1879b. Über die Korallen der Insel Ponape. J. Mus. Godeffroy, Hamburg 14: 201-212.

Bourne, G.C. 1905: On the solitary corals collected by Professor Herdman, at Ceylon, in 1902. Rep. Gov. Ceylon on Pearl Oyster Fish. of Gulf of Mannar, Suppl. Rep. 29: 187-242.

Chevalier, J.P. 1971. Les Scleractiniaires de la Melanesie francaise (Nouvelle Caledonie, Iles Chesterfield, Iles Loyaute, Nouvelles Hebrides). 1ere Partie. Exped. Francaise recifs coralliens Nouvelle Caledonie, Edn. Fond. Singer Polignac, Paris, 5: 5-307, pl. 1-38.

Chevalier, J.P. 1975. Les Scleractiniaires de la Melanesie francaise (Nouvelle Caledonie, Iles Chesterfield, Iles Loyaute, Nouvelles Hebrides). 2eme Partie. Exped. Francaise recifs coralliens Nouvelle Caledonie, Edn. Fond. Singer Polignac, Paris, 7: 1-407, pl. 1-42

Crossland, C. 1948. Reef corals of the South African coast. Ann. Natal Museum., 11(2): 169-205, pl. 5-14.

Crossland, C. 1952. Madreporaria, Hydrocorallinae, Heliopora and Tubipora. Sci. Rep. Great Barrier Reef Exped. 1928-29. Br. Mus. (Nat. Hist.) 6: 85-257, pls. 1-56.

Crossland, C.J. 1988. Latitudinal comparisons of coral reef structure and function. Proc. 6th Int. Coral Reef Symposium, Australia, Vol. 1: 221-226.

Dana, J.D. 1846-1849. Zoophytes. U.S. Exploring Exped. 1838-42, 7: 1-740, pls. 1-61.

Day, J.A. 1969. A guide to marine life on southern African shores. A. A. Balkema, Cape Town.

Dinesen, Z.D. 1977. The coral fauna of the Chagos Archipelago. Proc. Third Int. Coral Reef Symp., Miami: 155-161.

De Freitas, A. 1984. The Faneoidea of Southeast Africa. I. The study area and key to the southeast African species. Investigational Report Oceanographic Research Institute, Durban: 1-32.

Edwards, H. Milne & Haime, J. 1848. Note sur la classification de la deuxieme tribu de la famille des Astreides. C. R. Hebd. Seances Acad. Sci. 27(20): 490-497.

Edwards, H. Milne & Haime, J. 1849. Memoire sur les polypiers appartenant a la famille des Oculinides, au groupe intermediaire des Pseudastreides et a la famille des Fongides. C. R. Hebd. Seances Acad. Sci. 29: 67-73.

Edwards, H. Milne & Haime, J. 1857-1860. Histoire naturelle des Coralliaires. Paris 1,2 & 3: 1-326, 1-632, 1-560.

Ehrenberg, G.G. 1834. Beiträge zur physiologischen Kenntnis der Corallenthiere im allgemeinen und besonders des Roten Meeres. Abh. K. Akad. Wiss. Berlin 1832, 250-380.

Ellis, J. & Solander, D. 1786. The natural history of many curious and uncommon zoophytes. London, 1: 1-208, pls 1-63.

Eschscholz, J.F., von. 1925. Bericht über über die zoologische Ausbeute während der Reise von Kronstadt bis St.Peter und St.Paul. Zoophyten. Isis (Jena) 6: 734-747.

Esper, E. J. C. 1789-97. Die Pflanzenthiere 1, 97-192, 1789. Fortsetzungen 1: 1-64, 1794. 1: 65-116. 1795. 1: 169-230, 1797, Nürnberg.

Faure, G. 1977. Annotated Checklist of corals in the Mascarene Archipelago, Indian Ocean. Atoll Res. Bull. 203: 1-26.

Faure, G. & Pichon, M. 1978. Description de Favites peresi, nouvelle espece de Scleractiniaire hermatypique de l'ocean Indien (Cnidaria, Anthozoa, Scleractinia). Bull. Mus. natn. Hist. nat., Paris, 3e ser., No 513, Zoologie 352: 107-127.

Fisher de Waldheim, 1807. Description du Museum Demidoff. Moskow 3: 295-296, pl.4

Forskal, P. 1775. Descriptiones Animalium, Avium, Amphibiorum, Piscium, Insectorum, Vermium quae in itinere orientali observavit Petrus Forskal. XVIII-XIX: 131-139. Hauniae.

Gardiner, J.S. 1899. On the astraeid corals collected by the author in the South Pacific. Proc. Zool. Soc. Lond.: 734-764.

Gardiner, J.S. 1904. Madreporaria, I Introduction, II Astraeidae in "Fauna and Geography of the Maldives and Laccadives Archipelagoes". Cambridge, 2: 756-790, pls. 59-64.

Gray, J.E. 1847. An outline of an arrangement of stony corals. Ann. Mag. Nat. Hist. 19: 120-128.

Gregory, J.W., 1900. The corals. Jurassic fauna of Cutch. Palaeonthologia Indica (Calcutta) (9)2(2): 1-195, pl.2-27.

Hamilton, H.G.H. & W.H. Brakel. 1980. Structure and coral fauna of East African reefs. Bull. Mar. Sci. 34: 248-266.

Hoffmeister, J.E. 1925. Some corals from American Samoa and the Fiji Islands. Pap. Dep. mar. Biol. Carnegie Inst. Wash. (Publ. 340)22, 1-90, pl. 1-23.

Hoffmeister, J.E. 1929. Some reef corals from Tahiti. J. Wash. Acad. Sci. 19(16): 357-365, pls. 1-2.

Jokiel, P. & Martinelli, F.J. 1992. The vortex model of coral reef biogeography. Journal of Biogeography 19: 449-458.

Klunzinger, C.B. 1879. Die Korallenthiere des Roten Meeres. 2, 1-88, pl. 1-10; 3, 1-100, pl. 1-10, Gutmann, Berlin.

Koby, F., 1890. Monographie des polypiers jurassiques de la Suisse. Mem. Soc. Palaeontol. Suisse 16: 457-582, pl.122-130.

Lamarck, J.B.P. de. 1816. Histoire naturelle des animaux sans vertebre. Paris, 2: 1-568.

Lamouroux, J.V.F. 1821. Exposition methodique des ordres de polypiers avec les planches d'Ellis & Solander et quelques planches nouvelles. Paris. VIII: 1-115, pl.1-85.

Link, H.T. 1807. Beschreibung der Naturaliensammlungen der Universität zu Rostock. (3): 161-165.

Linnaeus, C. 1758. Systema naturae, Tomus I (Regnum animale). Holmia, Ed X, 824pp.

Linnaeus, C. 1767. Systema naturae, Tomus I, (Regnum animale), pars II. Holmia, Ed XII, p 793-798.

Marenzeller, E. von. 1901. Ostafrikanische Steinkorallen. Naturwiss. Ver. Hamburg. Ver. 3 Ser.: 117-134, 1pl.

Marenzeller, E. von. 1907. Expeditionen S.M. Schiff "Pola" in das Rote Meer. Zool. Ergeb. 25-Tiefseekorallen: 13-27, pl.1-2; Riffkorallen: 27-97, pl. 1-29. Denkschr. Akad. Wiss. XXVI Wien 80.

Matthai, G. 1914. A revision of the recent colonial Astraeidae possessing distinct corallites. Trans. Linn. Soc. Lond. 2nd Ser. Zool. 17: 1-140, pl. 7-38.

Matthai, G. 1923. Madreporaires de la Nouvelle Caledonie. Bull. Biol. Fr. Belg.: 70-88, pl. 1-2.

Matthai, G. 1928. A monograph on the recent meandroid Astraeidae. Cat. Madreporarian Corals Br. Mus. (Nat.Hist.) 7: 1-288, pl.1-72.

Nemenzo, F. 1959. Systematic studies on Philippine shallow-water scleractinians. II Suborder Faviida. Nat. Appl Sci. Bull. Philippines, 16(1-4): 73-135.

Oken, L. 1815. 1. Zunft Edelkorallen, Steinkorallen. Lehrbuch der Naturgeschichte, Dritter Theil, Zoologie, Erste Abtheilung, Fleischlose Thiere: 59-74, Schmid, Leipzig, Jena.

Ortmann, A. 1888. Studien über die Systematik und geographische Verbreitung der Steinkorallen. Zool. Jahrb. Abt. Syst. Geogr. Biol. Tiere 3, 143-788.

Ortmann, A. 1889. Beobachtungen an Steinkorallen von der Südküste Ceylons. Zool. Jahrb. Abt. Syst. Geogr. Biol. Tiere 4: 493-590, pl. 11-18.

Ortmann, A. 1892. Die Korallenriffe von Dar es Salaam und Umgegend. Zool. Jahrb. Abt. Syst. Geogr. Biol. Tiere 7, 7: 631-670.

Pichon, M. 1964. Contribution a l'etude de la repartition des Madreporaires sur le recif de Tulear, Madagascar. Rec. Trav. Stn. Mar. Endoume-Mars. fasc. hors ser. suppl. 2, 78-203.

Pillai, C.S.G. & Scheer, G. 1973. Bemerkungen über einige Riffkorallen von Samoa und Hawaii. Zool. Jahrb. Abt. Syst. Oekol. Geogr. Tiere, 100: 466-476.

Pillai, C.S.G. & Scheer, G. 1976. Report on the stony corals from the Maldive Archipelago. Zoologica (Stuttgart) Heft 126: 1-83, pls. 1-23

Quelch, J.J, 1884. Preliminary notice of new genera and species of Challenger reef-corals. Ann. Mag. Nat. Hist. 85)13: 292-297.

Quelch, J.J., 1886. Report on the reef corals collected by H.M.S. Challenger during the years 1873-1876. Report on scientific results of voyage of H.M.S. Challenger. Zoology 16: 1-203, pl. 1-12.

Quoy, J.R.C. & J.P. Gaimard, 1833. Zoophytes. in: Voyage de decouvertes de l'Astrolabe, execute par ordre du roi, pendant les annees 1826-29, sous commandement de M.J. Dumont d'Urville. M.J.Dumont d'Urville, ed. Zoologie 4: 175-254, pl. 14-20.

Ramsey, P.M. & Mason, T.R., 1990. Development of a type zoning model for Zululand Coral Reefs, Sodwana Bay, South Africa. J. Coastal Res. 6(4): 829-852.

Rosen, B.R. 1971. Annotated check list and bibliography of corals of the Chagos Archipelago (including the recent collection from Diego Garcia), with remarks on their distribution. Atoll Reserch Bulletin 149:67-88.

Rosen, B.R. 1984. Reef coral biogeography and climate through the late Cainozoic: just islands in the sun or a critical pattern of islands? In: Fossils and climate. P.J. Benchley (ed.). Wiley, Chichester: 201-262.

Rosen, B.R. 1988. Progress, problems and patterns in the biogeography of reef corals and other tropical marine organisms. Helgol. Meeresunters. 42: 269-301.

Scheer, G. & Pillai, C.S.G. 1974. Report on the Scleractinia From the Nicobar Islands. Zoologica (Stuttg.) Heft 122:1-75, pls. 1-33.

Scheer, G. & Pillai, C.S.G. 1983. A Report on the Stony Corals of the Red Sea. Zoologica (Stuttg.) Heft 133: 1-197.

Schweigger, A.F., 1819. Beobachtungen auf naturhistorischen Reisen - Anatomisch-physiologische Untersuchungen über Corallen. Berlin.

Schuhmacher, H. 1984. Reef-building properties of Tubastrea micranthus (Scleractinia, Dendrophylliidae), a coral without zooxanthellae. Mar. Ecol. Progr. Ser. 20: 93-99.

Schuhmacher, H. 1991. Korallenriffe. Verbreitung, Tierwelt, Ökologie. 2nd edition, BLV Verlagsgesellschaft München.

Sheppard, C.R.C. 1987. Coral species of the Indian Ocean and adjacent seas: a synonymized compilation and some regional distribution patterns. Atoll Research Bulletin 307: 1-32.

Sheppard, C.R.C. & Salm R.V. 1988. Reef and coral communities of Oman, with a description of a new coral species (Order Scleractinia, genus Acanthastrea). J. Nat. Hist. 22: 263-279.

Sheppard, C.R.C. & Sheppard A.L.S. 1991: Corals and coral communities of Arabia. Fauna of Saudi Arabia, Vol.12: 3-170.

Studer, T. 1881. Beiträge zur Fauna der Steinkorallen von Singapore. Mitt. Naturforsch. Ges. Bern (1880) 979: 15-53.

Van Ofwegen L.P. & Y. Benayahu. 1992. Notes on Alcyonacea (Octocorallia) from Tanzania. Zool. Meded. Leiden 66(6): 139-154, figs. 1-15..

Vaughan, T.W. 1918. Some shoal-water corals from Murrey Islands, Cocos Keeling Islands and Fanning Islands. Pap. Dep. mar. Biol. Carnegie Inst. Wash. 9 (Publ.213), 51-234, pl. 20-93.

Vaughan, T.W. & Wells, J.W. (1943). Revision of the suborders, families and genera of the Scleractinia. Geol. Soc. Am. Spec. Pap. 44: 1-363, pl. 1-51.

Veron, J.E.N., Pichon, M. & Wijsman-Best, M. 1977. Scleractinia of Eastern Australia, Part II, Families Faviidae, Trachyphyllidae. Aust. Inst. Mar. Sci. Monogr. Ser., Vol.3: 1-205, pls. 1-406.

Veron, J.E.N. & Pichon, M. 1982. Scleractinia of Eastern Australia, Part IV, Family Poritidae. Aust. Inst. Mar. Sci. Monogr. Ser., Vol.5:136,137.

Veron, J.E.N. 1986. Corals of Australia and the Indo Pacific. Angus and Robertson Publishers, North Ryde: 443-535.

Veron, J.E.N. & Marsh, L.M. 1988. Hermatypic corals of Western Australia. Records and annotaed species list. Rec. Western. Aust. Museum, Supplement No. 29: 1-137.

Veron, J.E.N. 1990.Re-examination of the reef corals of Cocos (Keeling) Atoll. Rec. West. Aust. Mus. 14(4): 553-581.

Verrill, A.E. 1902. Notes on the coral genus Acropora (Madrepora Lam.) with new descriptions and figures of types and of several new species. Trans. Connecticut Acad. Arts. Sci.11: 207-77, 7 pls.

Verrill, A.E. 1864. List of the polyps and corals sent by the Museum of Comparative Zoology to other institutions in exchange, with annotations. Bull. Mus. Comp. Zool. Harv. Coll. 1, 29-60.

Wells, J.W. 1954. Recent corals of the Marshall Islands. Prof. Pap. US Geol. Surv. 260, I: 385-486, pls. 94-122.

Wells, J.W. 1956. Scleractinia. in: Moore, R.C. (ed.): Treatise on Invertebrate Palaeontology. Coelenterata. Univ. Kansas Press. F: 328-440.

Wijsman-Best, M. 1972. Systematics and ecology of New Caledonian Faviinae (Coelenterata, Scleractinia). Bijdr. Dierk. 42(1): 1-76, pls. 1-14.

Wijsman-Best, M. 1974. Faviidae collected by the Snellius Exped. I: The Genus Favia. Snellius Exped. 25, Zool. Meded. Rijksmus. Nat. Hist. Leiden 48(22): 249-261, pls.1-14.

Wijsman-Best, M. 1976. Faviidae collected by the Snellius Expedition II. The genera Favites, Goniastrea, Platygyra, Oulophyllia, Leptoria, Hydnophora and Caulastrea. Snellius Exped. 27, Zool. Meded. Rijksmus. Nat. Hist. Leiden 50(4): 45-63, pl. 1-8.

Wijsman-Best, M. 1977. Indo-Pacific coral species belonging to the subfamily Montastreinae Vaughan & Wells, 1943 (Scleractinia, Coelenterata). Part I. The genera Montastrea and Plesiastrea. Zool. Meded. Rijksmus. Nat. Hist. Leiden.

Wijsman-Best, M., Faure, G. & Pichon, M. 1980. Contribution to the knowledge of the stony corals from the Seychelles and Eastern Africa. Rev. Zool. afr. 94(3): 600-627, pls.IX-XII.

Yabe, H. & Sugiyama, T. 1935. Revised lists of the reef corals from the Japanese seas and of the fossil reef corals

of the raised reefs and the Ryukyu limestone of Japan. J.Geol.Soc.Jpn. 42: 379-403.

Yabe, H., Sugiyama, T. & Eguchi, M. (1936). Recent reef building corals from Japan and the South Sea islands under Japanese mandate. I. Sci. Rep. Tohuku Univ. second Ser. (Geol.), Spec. vol. 1, 1-66, pl. 1-59.

P A R T II

The Patterns: Community analysis

In this part of the thesis, I examine the patterns underlying the coral communities in Northern Natal. This then allows formulation of hypotheses about their ecological functioning and the major abiotic forcing factors shaping this system, some of which are examined in more detail in Part III.

WAVE ACTION, SEDIMENTATION AND THE STRUCTURE OF AFRICA'S SOUTHERNMOST CORAL COMMUNITIES

Abstract

The community structure on Africa's southernmost coral communities, which grow on submerged fossil dune and beachrock systems and do not form true coral reefs, was quantitatively investigated by means of line transects and phototransects. A major difference from typical reef systems was in the absence of any noticeable reef accretion. None of the typical geomorphological reef-zones such as lagoons, reef crests or reef slopes were developed. The absence of ecological differentiation caused by topographical differentiation has given rise to a very uniform community structure, differentiated only into two major community-types with three subcommunities. Typical fossil sand dunes and shallow fossil beach rock platforms were dominated by soft-corals and differed from deep sandstone outcrops, which were dominated by hard corals. A high proportion of soft-corals was found in shallow communities (40-60%). Distinct subcommunities, which were found on most reefs, were a soft-coral dominated "reef-top" community in areas of low sedimentation, dominated by the genera Sinularia and Lobophytum, and a hard-coral dominated "gully" community (predominantly Montipora and Faviidae), in areas of high sedimentation. A deep sponge-dominated sub-community was found on the deepest outcrops. The lower limit for most coral growth was between 35 & 40m. Community structure suggests depth, wave action and sedimentation to be the major factors influencing these communities. Ninety species of hard-corals, mostly of typical Indo-Pacific distribution, were found.

Introduction

The southernmost reef coral communities on the African continental coast are situated along the Maputaland coastline in northern Natal, South Africa, at 27°50'S. This rates them among the southernmost true reef coral communities found anywhere in the world (the southernmost being at Lord Howe Island, off Australia at 31°33'S). The faunistic analysis and the taxonomic revisions in Part I showed that the hard and soft corals which dominate the hard bottom communities in Maputaland are mostly typical Indo-Pacific coral reef taxa. The substrata on which they thrive, however, are not true coral reefs but fossilized and submerged dune systems (Ramsey & Mason, 1990). They do not break the surface and lack most geomorphological traits typical of true coral reefs, which normally lead to differentiation of coral communities (Stoddart, 1969; Loya, 1972; Done, 1982; Sheppard, 1982). None of the usual features (lagoons, reef crests or steep reef slopes) are developed, thus resulting in relatively homogenous topographic conditions over most of the hard bottom area covered by corals. The major topographical features are gullies and associated small drop-offs, perpendicular to the dominant direction of the swells. While the southerly location of these coral communities in itself calls for a detailed study, the geological setting, within which these corals live, adds further interest to the study of this particular system. In the absence of the usual topographical features found on true coral reefs, which create a range of environments and coral communities (Done, 1982; Sheppard, 1982; Dinesen, 1983), it is of interest whether and how the South African reefs achieve any differentiation of coral communities.

This study provides information about 1) the coral fauna of the region, 2) the coral cover and abundance, 3) community differentiation on a macro (inter-reef) and micro (within-reef) scale and 4) suggestions about the major environmental factors influencing these southernmost reef coral communities in Africa.

Material and methods

Data were collected using the line transect method with continuous transect recording (Loya, 1978), combined with phototransects. The ideal length of the transects was tested prior to sampling by means of a species-per-area curve (Loya, 1978) and varied between 10 and 14m. For reasons of comparability with other studies, which used 10m-long line transect, 10m transects were also used in the present study. Due to the large and morphologically very uniform area which was covered by coral growth, sample sites were repeatedly chosen at random on each investigated reef. At each sample site a series of 10 transects with a spacing of one metre was recorded. This procedure was repeated in different, randomly chosen sites on each reef in order to provide replicate samples. Phototransects, covering areas of 4x10m each, were also taken. By means of a standardized conversion it was possible to gain further line-transect information from the photo-transects. The scale of the photographs was determined using markings on a transect line, a portion of which was present in each photograph. Coral intercepts on the transect line were measured using a ruler, the data were then multiplied by a previously determined scale factor to obtain an estimate of the actual intercept distances.

Not only coral intercepts and the intercepts of other major invertebrate groups, such as sponges and ascidians were recorded

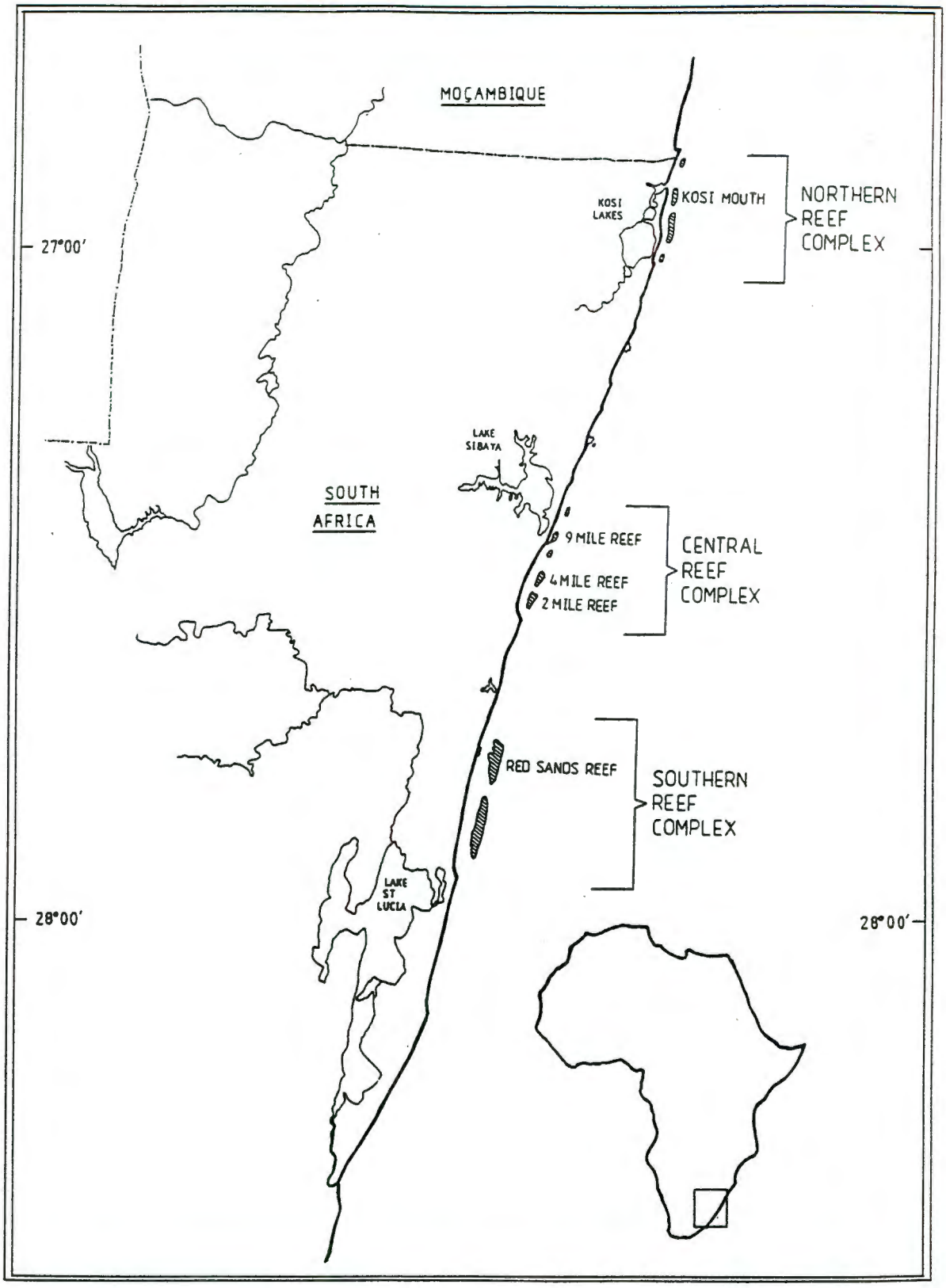


Fig. 1: Location of the Maputaland reef complexes in northern Natal, RSA, which are the southernmost reef coral communities in Africa. Community analysis was performed on selected reefs indicated by their local name.

but also the intercepts of sand and unoccupied rock. Unoccupied rock was defined as rock without any growth of macroalgae or invertebrates.

The position of each transect on the reefs, i.e. whether it was located on a flat horizontal area, a ridge, a drop-off, a gully-edge or inside a gully, was recorded. Fig. 2 explains the terminology used. It was also recorded whether transects were exposed to heavy water motion or whether they were sheltered. All transects deeper than 20m were automatically considered sheltered. Shallow transects were only considered sheltered if situated in locations where topography made high water movement unlikely.

A total of 171 transects were recorded (Northern Reef Complex: Kosi Reef 6; Central Reef Complex: 2-Mile Reef 52, 4-Mile Reef 63, 9-Mile Reef 30; Southern Reef Complex: Red Sands Reef 20). Data were evaluated following the method of Field et al. (1982) mostly using a statistical package developed by Clarke & Warwick (pers.comm.). Data were root-root transformed and subjected in a first step to correspondence analysis and then to agglomerative, hierarchical cluster analysis using the Bray-Curtis Dissimilarity Index, grouping by group average. They were then subjected to ordination by Multidimensional Scaling (MDS), using the same distance matrix as for the classification. Environmental variables were superimposed on the groupings obtained by MDS in order to visualize their influence on species grouping. Dominant species were measured by their contribution to the average Bray-Curtis dissimilarity between groups (Field et al., 1982, Clarke & Warwick, pers.comm.).

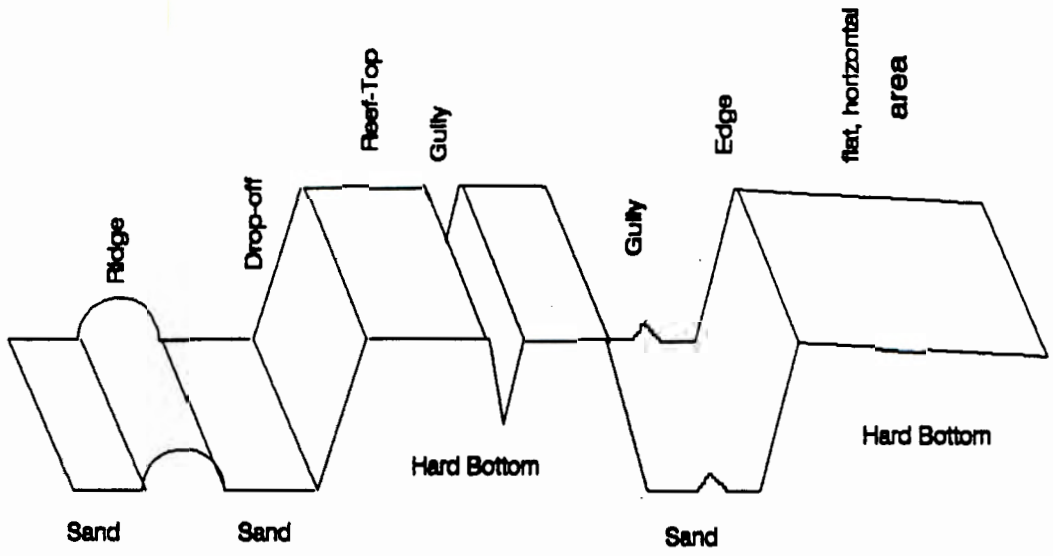


Fig. 2: Explanation of terms used to describe the position of transects on the reefs. The situation is idealized.

Indices used were the Shannon-Weaver diversity index H' (Loya, 1972) and its according evenness measure (Pielou, 1975) as well as Simpson's Alpha as a dominance measure (Brower & Zar, 1977).
Sedimentation rates were measured using open topped tubes of 11cm bore, each of which projected by 15 cm from a rectangular vinyl containers (20x10cm) that served to accumulate sediments settling in the tube. Suspended sediment in the water was sampled with 5-litre sampler bottles with simultaneously closing lids on both ends.

Study area

The coral communities studied grow on submerged fossil dune or beachrock systems (Ramsey & Mason, 1990) which are situated from about 100 to 1000m off-shore. The topography of the individual reefs is mostly flat, with numerous gullies and occasional drop-offs (rarely more than 6m) to the surrounding sea floor. The area covered by these outcrops varies from a few hundred square meters to several square kilometers.
The depth range of the coral-covered fossil dunes varies from an average 8-10m shallowest depth, although in some instances individual pinnacles rise to about 4m depth, to about 35-40m at their foot (2-Mile Reef, Red Sands Reef). The average slope of the dune face is less than 5°. Flat dunes (4-Mile Reef, Kosi Reef) are situated between 18 and 24m; beachrock platforms (9-Mile Reef) between 6 and 18m with a steep drop-off between 12 and 18m parallel to the shoreline.
The reefs can be grouped into a Northern, a Central and a Southern Reef Complex (Fig. 1). The Southern Reef Complex comprises the southernmost reef-coral communities on the African coast. Emphasis

was laid on the study of reefs in the Central Reef Complex in the Sodwana Bay area. Smaller samples were obtained for comparative purposes from the Northern and Southern Reef Complexes.

The Maputaland coastline is exposed to open oceanic swells of the SW and South Indian Ocean. Tidal range is between 1m at neaps and 2m at spring tides (Schumann & Orren, 1980).

Although the topography of most areas was very uniform, the sandstone outcrops were separated into (1) higher-lying, largely sediment free areas, (2) shallow gullies and depressions with little resident sediment but high debris and sediment movement in heavy seas, and (3) deep gullies with large amounts of resident sediment.

Results

a) Species richness, diversity and composition

All encountered hard corals were identified to species level but only the common soft-coral taxa were identified. A detailed account of the soft-coral fauna can be found in Benayahu (in press).

A total of 90 species of Scleractinia and one species of hermatypic Hydrozoa were found, most of which were new distribution records for the area (Tab. 1, see also Part I, Chapter 8), as no comprehensive species list for the area has been available (Boshoff, 1980, Ramsey and Mason, 1990).

Overall, hard corals occupied slightly more space on the reefs than soft-corals (Tab. 2) and hard and soft corals collectively were by far the most dominant members in most of the benthic invertebrate communities.

1) Psammocora profundacella Gardiner
2) Stylophora pistillata Esper
3) Pocillopora damicornis L.
4) P. verrucosa Ell.& Sol.
5) P. eydouxi Ed.& H.
6) Montipora venosa (Ehrgb)
7) M. tuberculosa (Lam.)
8) M. verrucosa (Lam.)
9) M. danae Ed.& H.
10) M. monasteriata (Forsk.)
11) M. aequituberculata Bernard
12) M. spongodes Bernard
13) M. turgescens Bernard
14) Acropora palifera (Lam.)
15) A. humilis (Dana)
16) A. clathratha (Brook)
17) A. nasuta (Dana)
18) A. tenuis (Dana)
19) A. austera (Dana)
20) A. aculeus (Dana)
21) A. latistella (Brook)
22) A. millepora (Ehrbg.)
23) A. danai (Ed.& H.)
24) A. horrida (Dana)
25) A. hyacinthus (Dana)
26) A. anthocercis (Brook)
27) A. florida (Dana)
28) Astreopora myriophthalma (Lam.)
29) Pavona clavus (Dana)
30) P. minuta (Wells)
31) Gardineroseris planulata (Dana)
32) Pachyseris speciosa (Dana)
33) Leptoseris explanata Yabe & Sug.
34) Coeloseris meyeri Vaughan
35) Coscinaraea monile (Forsk.)
36) C. cf.columna (Dana)
37) Anomastrea irregularis v.Marenz.
38) Horastrea indica Pichon
39) Podabacia crustacea (Pallas)
40) Fungia (Pleuractis) scutaria Lam.
41) Cycloseris cyclolites (Lam.)
42) C. costulata Ortmann
43) C. cf.marginata Boschma
44) Diaseris distorta (Michelin)
45) Goniopora djiboutensis Vaughan
46) G. somaliensis Vaughan
47) Porites lichen Dana
48) P. lutea Ed.& H.
49) P. solida (Forsk.)
50) Alveopora allingi Hoffm.
51) A. spongiosa Dana
52) Favia favus (Forsk.)
53) F pallida (Dana)
54) F. speciosa (Dana)
55) F. laxa (Klunz.)
56) F. matthai Vaughan
57) F. rotumana (Gardiner)
58) F. stelligera (Dana)
59) Favites pentagona (Esper)
60) F. abdita (Ell.& Sol.)
61) F complanata(Ehrbg.)
62) F. peresi Faure & Pichon
63) F. flexuosa (Dana)
64) F. halicora (Ehrbg.)
65) Goniastrea pectinata (Ehrbg.)
66) G. retiformis (Lam.)
67) G. edwardsi Chevalier
68) Platygyra daedalea (Ell.& Sol.)
69) Oulophyllia crispa (Lam.)
70) Leptastrea purpurea (Dana)
71) L. sp.1
72) Cyphastrea chalcidicum (Forsk.)
73) Echinopora hirsutissima Ed.& H.
74) E. gemmacea (Lam.)
75) Montastrea annuligera (Ed.& H.)
76) Plesiastrea versipora (Ed.& H.)
77) Hydnophora exesa (Pallas)
78) H. microconos (Lam.)
79) Galaxea fascicularis (L.)
80) Acanthastrea echinata (Dana)
81) A. simplex (Crossl.)
82) Lobophyllia corymbosa (Forsk.)
83) Scolymia cf. vitiensis Bruegg.
84) Blastomussa merletti Wells
85) Gyrosmilia interrupta Ehrbg.
86) Turbinaria mesenterina (Lam.)
87) Tubastrea coccinea Lesson
88) Dendrophyllia micranthus Ehrbg.
89) Tubipora musica L.
90) Millepora platyphylla (Hemp.)

Tab. 1: List of all hermatypic hard coral species found in the transects during this study.

Among the hard-corals the Acroporidae covered most space overall (16.2%), followed by the Faviidae (13.8% of total hard-coral coverage). The Faviidae were consistantly more common than the Acroporidae, which dominated only Kosi-Mouth and Four-Mile Reef (Tab.3).

Among the soft-corals Lobophytum (20.6%) and Sinularia (16.3%) were the dominant space utilizers (Tab. 3).

The most diverse coral community was encountered on 4-Mile Reef (H'=2.24±0.36) followed by Red Sands Reef (H'=2.14±0.25) and Kosi Bay Reef (H'=2.11±0.36). The least diverse communities were found on 2-Mile and 9-Mile Reefs (H'=2.01±0.36, H'=2.01±0.33 respectively).

b) Between-reef differentiation

The ordination of all recorded transects by means of correspondence analysis showed a clear differentiation into two groups of samples along two axes perpendicular to each other (Fig. 3). The two transect clusters were elongate and poorly defined in their central part, where overlap existed. Cluster A, stretched mainly along the negative axis 1, comprised exclusively transects from Four-Mile Reef and Kosi-Mouth Reef, while cluster B, differentiating mostly along the positive axes 1 and 2, was made up from transects from Two-Mile-, Red-Sands- and Nine-Mile Reefs.

The differentiation axes could be best explained as representing the non-soft-coral component in the data. The dense cloud of data points in the central part of the graph represents transects with an almost equal contribution by hard- and soft-corals to total living coverage. Cluster A differentiated along increasing hard coral contribution, mainly by the genus Acropora, cluster B

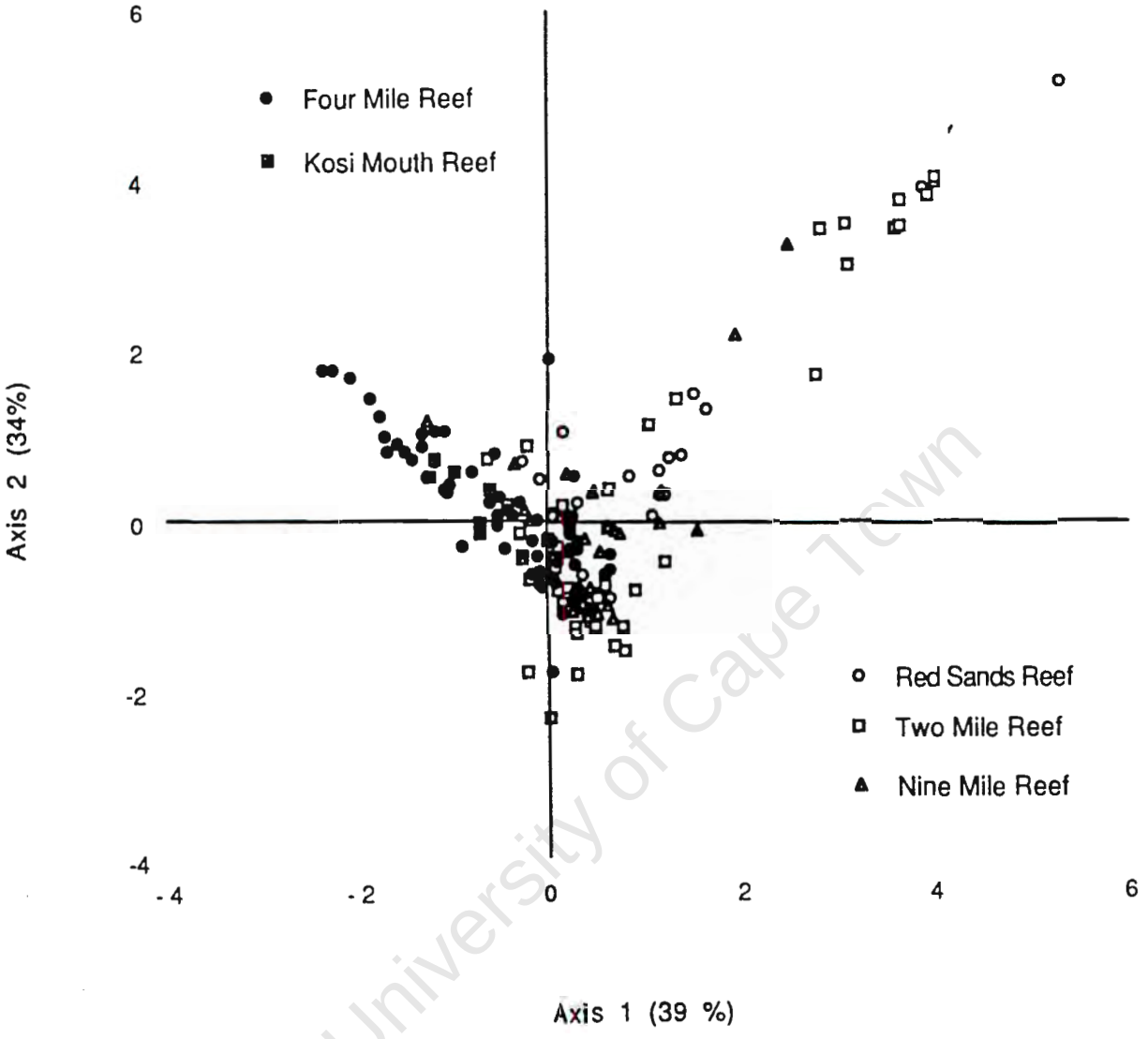


Fig. 3: Ordination by correspondence analysis of all transects obtained from 5 reef sites in Northern Natal. Two distinct clusters are formed, suggesting two different community types.

	Total	Kosi	9-Mile	4-Mile	2-Mile	Red Sands
Soft corals	41.8 ±7.80	35.3 ±20.3	54.1 ±27.9	34.8 ±15.9	43.1 ±23.2	41.7 ±18.1
Hard corals	50.5 ±11.5	62.1 ±19.2	38.6 ±24.1	63.4 ±17.1	45.1 ±21.3	43.2 ±16.5
Sponges	5.70 ±4.80	0.08 ±1.60	5.60 ±11.1	1.70 ±2.90	10.0 ±17.9	10.9 ±14.0
Ascidians	3.70 ±3.90	1.70 ±2.80	1.90 ±6.60	0.03 ±0.20	2.10 ±4.50	3.70 ±6.50
Total cover	57.4 ±14.8	76.3 ±8.06	53.6 ±19.6	67.9 ±20.8	50.3 ±22.6	38.9 ±13.2

Tab. 2: Space utilisation by the major invertebrate categories on the Maputaland reef complexes expressed as percent share of total living animal coverage as calculated from intercepts on the line transects.

	Kosi	9-Mile	4-Mile	2-Mile	Red Sands
Acropora	35.03%	9.9%	25.2%	6.2%	4.9%
Montipora	5.8%	3.5%	7.6%	9.7%	2.6%
Faviidae	9.2%	15.4%	15.1%	12.1%	17.2%
Sinularia	5.3%	25.8%	11.8%	27.7%	11.1%
Lobophytum	27.7%	23.3%	13.6%	16.7%	21.8%

Tab. 3: Space utilisation by the major hard and soft coral families and genera on the Maputaland reef complexes expressed as percent share in total living coverage calculated from intercepts on the line transects.

differentiated along an axis of increased contribution to coverage by sponges and tunicates. This situation is also illustrated by table 2.

Tables 2 and 3 further indicate similarity between the reefs within each of these clusters concentrating on the relative importance of hard- and soft coral cover and the proportional importance of the dominant genera. On Kosi Mouth Reef and Four-Mile reef hard corals covered more than 60% of utilized space, the genus Acropora being by far the most dominant, while soft corals covered less than 40%. On 2-Mile and Red Sands Reef both coral groups were roughly equal in their share of total coverage. Only on Nine-Mile reef were soft corals clearly dominant (Table 2). On these three reefs (Two-Mile, Nine-Mile, Red-Sands-Reef) the Faviidae were the dominant hard corals and either Sinularia or Lobophytum the dominant soft corals. Therefore two different community types existed: Four-Mile and Kosi-Mouth Reefs had a similar community structure which differed from that observed on Two-Mile, Red-Sands and Nine-Mile Reefs. This means that primary differences in the coral community structures existed between the deep outcrops (Kosi Mouth Reef, Four-Mile Reef) and the fossil dunes (Two-Mile Reef, Red Sands Reef) and submerged beachrock platforms (Nine-Mile Reef). Therefore I evaluated the community structures within each reef type seperately. For each of these reef types one representative area was sampled in detail in the Central Reef Complex.

b) Within-community differentiation - the deep outcrops

Representative areas for this substratum type were sampled at Four-Mile Reef.

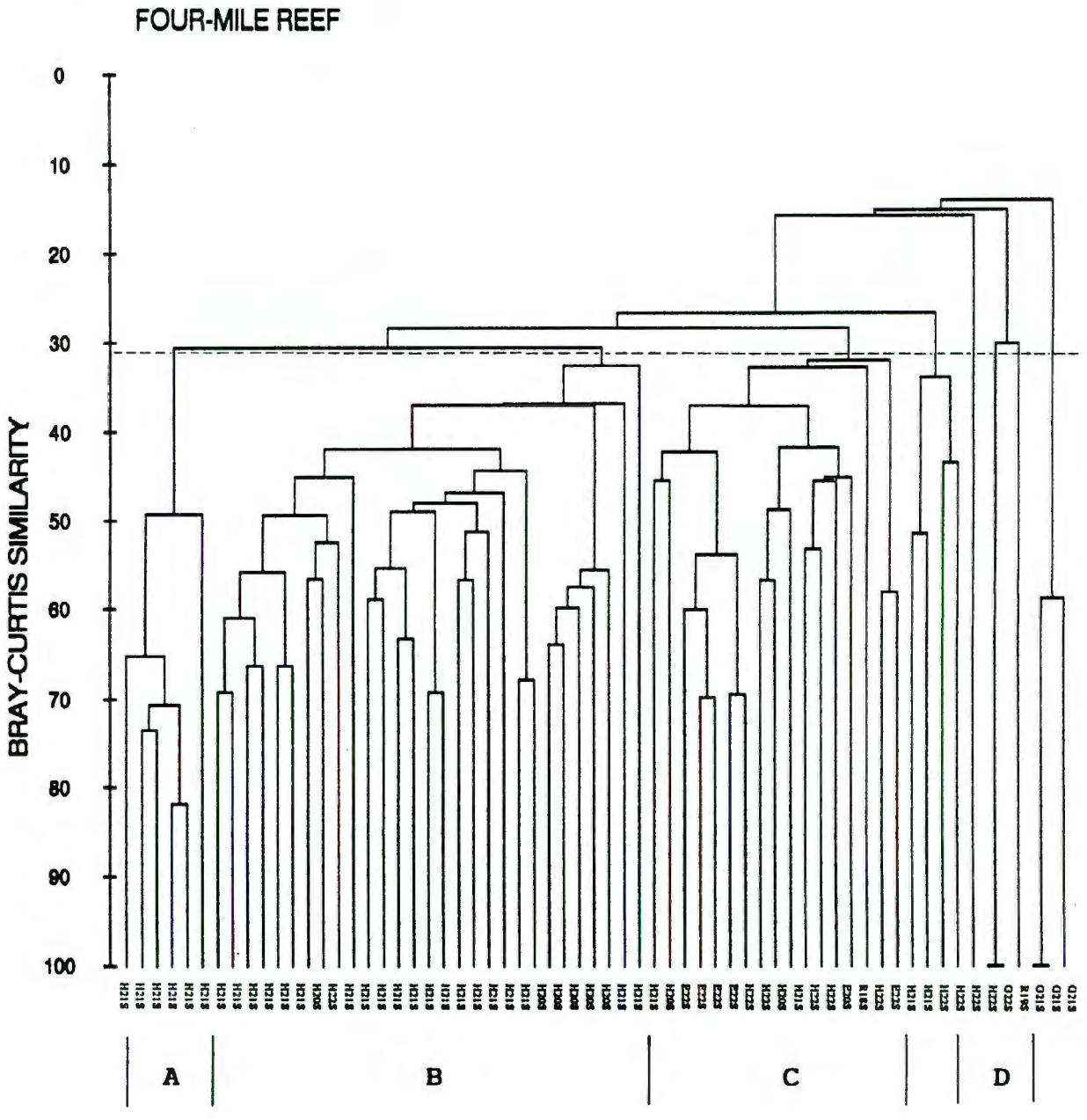


Fig. 4: Differentiation of the coral community on the deep outcrops (4-Mile Reef) as obtained by classification of quantitative data of all transects. 4 main groups (1-4) were distinguished at an arbitrary similarity level of 31% (y-axis). Species responsible for within-group similarity and beween-group dissimilarity are given in table 4. Transects are coded, characterizing their position on the reef. H=flat, horizontal area, G=gully, E=gully-edge, R=ridge, the number stands for depth in metres, S=sheltered (H22S: transect from horizontal part, 22m depth, sheltered location).

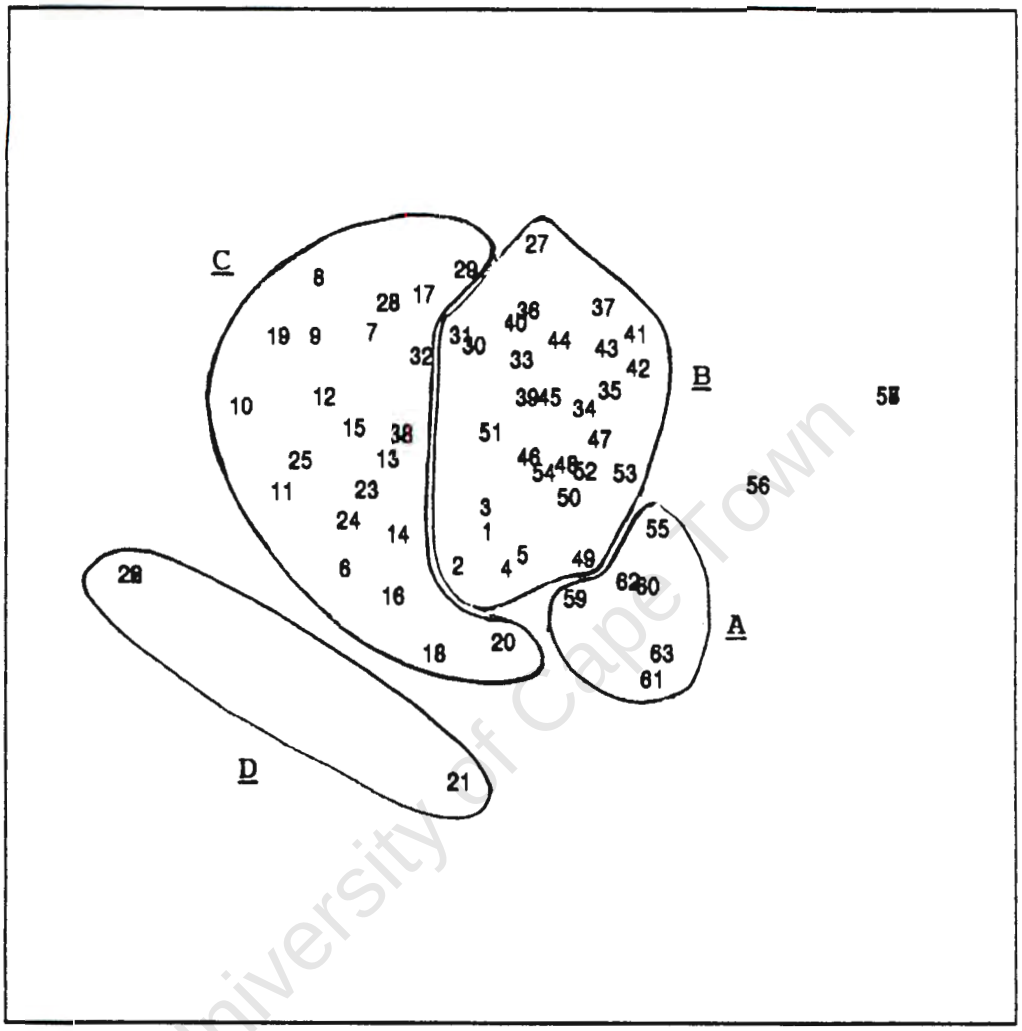


Fig. 5: Ordination of the 4-Mile Reef transects in 2 dimensions using multi-dimensional scaling on the same similarity matrix as Fig.4. The groups obtained by the dendrogram were superimposed onto the ordination plot by encircling each cluster of stations.

Hard corals dominated the community composition as could be seen by their high share of utilized space (Tab. 2). The dominant hard corals belonged to the family Acroporidae, with Acropora occupying far more space than Montipora (Tab. 3).

The classification of the transects, based on root-root transformed data, gave four distinct groups at the arbitrarily drawn 30% dissimilarity level (Fig.4). Group A was the most homogenous cluster, with an average similarity of 63%. The other clusters all had average similarities of less than 50% (group B: 41,8%, group C: 38.9%, group D: 38.4%). The ordination by Multidimensional Scaling (Fig. 5), which used the same similarity matrix as the classification, gave essentially the same results as the classification. Three groups of transects made up distinct clusters. A few transects did not fit into any cluster, being well seperated from the rest of the samples.

Indicator species for the clusters are given in Table 4. No species could be counted as a "perfect indicator", i.e. being exclusive to only one cluster (Field et al., 1982). Most species occurred in at least two of the four groups, the differences between the groups being based mainly on differences in abundance of the indicator species.

Superimposing environmental variables onto the ordination plot (Fig. 6 a-e) allowed conclusions to be drawn about the most important substratal and environmental factors influencing similarity between transects (as described below for each transect group).

Group A was mainly dominated by hard corals. The most dominant corals were Acropora clathrata, which formed solid, tabular or vasiform plates of up to 1.5m diameter, and Acropora austera, a

FOUR-MILE REEF			
Group A		**Differences between groups A&B**	
1) Acropora clathrata	(22.2%)	1) Stereonephthya sp.	(6.13%)
2) Acropora austera	(40.2%)	2) Oulophyllia crispa	(11.4%)
3) Stereonephthya sp.	(53.8%)	3) Sarcophyton spp.	(16.4%)
4) Oulophyllia crispa	(66.2%)	4) Acropora clathrata	(21.4%)
5) Lobophytum sp.4	(76.3%)	5) Acropora tenuis	(25.5%)
Group B		**Differences between groups B&C**	
1) Sarcophyton spp.	(17.5%)	1) Acropora tenuis	(3.65%)
2) Lobophytum venustum	(27.3%)	2) Acropora austera	(7.29%)
3) Acropora tenuis	(34.9%)	3) Sarcophyton spp.	(10.8%)
4) Acropora clathrata	(42.2%)	4) Favites pentagona	(14.3%)
5) Sinularia gyrosa	(49.4%)	5) Acropora clathrata	(17.6%)
Group C		**Differences between groups A&C**	
1) Favites pentagona	(11.4%)	1) Acropora austera	(6.22%)
2) Lobophytum venustum	(20.5%)	2) Stereonephthya sp.	(11.1%)
3) Montipora danae	(27.4%)	3) Acropora clathrata	(15.6%)
4) Montipora tuberculosa	(33.7%)	4) Favites pentagona	(19.6%)
5) Sinularia gyrosa	(39.7%)	5) Lobophytum sp.4	(23.5%)
Group D		**Differences between groups A&D**	
1) Lobophytum patulum	(18.3%)	1) Acropora austera	(7.04%)
2) Sarcophyton spp.	(35.9%)	2) Acropora clathrata	(12.9%)
3) Lobophytum sp.4	(47.6%)	3) Stereonephthya sp.	(18.6%)
4) Lobophytum depressum	(56.4%)	4) Oulophyllia crispa	(22.8%)
5) Echinophyllia aspera	(64.6%)	5) Sarcophyton spp.	(26.9%)
Differences between groups B&D		**Differences between groups C&D**	
1) Lobophytum venustum	(4.03%)	1) Lobophytum patulum	(4.52%)
2) Lobophytum patulum	(7.89%)	2) Lobophytum sp.4	(8.92%)
3) Lobophytum sp.4	(11.7%)	3) Lobophytum venustum	(12.7%)
4) Acropora tenuis	(15.4%)	4) Montipora danae	(15.9%)
5) Acropora austera	(19.1%)	5) Sarcophyton spp.	(19.1%)

Tab. 4: Species causing within group similarity and between group dissimilarity in the coral community on Four-Mile Reef. Species are listed in descending order according to their contribution to average Bray-Curtis similarity within groups or dissimilarity between groups. The numbers in brackets are cumulative values for contribution to average Bray-Curtis similarity or dissimilarity.

species with open arborescent branching pattern, forming monospecific thickets up to several metres in diameter. The horizontal projection of the platelike A. clathrata colonies on the transect line frequently formed a canopy over adjacent colonies, thus creating areas of greater than 100% surface cover. Group A comprised transects only from horizontal, flat parts of the reef (Fig.6d). Coral coverage was high ($\bar{x}$=79.9±2.99%) with medium amounts of bare rock ($\bar{x}$=20.1±2.99%) and no sand (Figs.6 a-e). Within this group average Shannon-Weaver diversity was relatively low ($\bar{x}$=1.69±0.99), with corresponding low evenness ($\bar{x}$=0.39±0.02) and high dominance index values ($\bar{x}$=0.25±0.03), which gave a clear picture of the importance of the dominant species.

Group B showed mixed dominance by soft and hard-corals, with soft corals being slightly more important (genera Sarcophytum, Lobophyton, Sinularia). Of all groups, B and A were the most similar (average dissimilarity=69.8%), and shared one of the indicator species, the hard coral A. austera (Tab. 4). Group B was also a community of the flat, horizontal parts of the reef (Fig.6d) with high average coral cover ($\bar{x}$=77.5±2.26%, Fig.6a), a medium proportion of free rock ($\bar{x}$=22.1±2.15, Fig.6b) and almost no resident sand ($\bar{x}$=0.36±0.36%, Fig.6c). Average diversity (x=2.29+0.04) and evenness ($\bar{x}$=0.53±0.009) were high, coupled with low dominance index values ($\bar{x}$=0.13±0.007), which indicated a very heterogenous community.

Group C was more hard-coral dominated than any other cluster, some of its hard coral indicators being uncommon or absent in all the other samples (e.g. Montipora danae, M. tuberculosa, Tab. 4). There was still a strong soft-coral component (Lobophytum

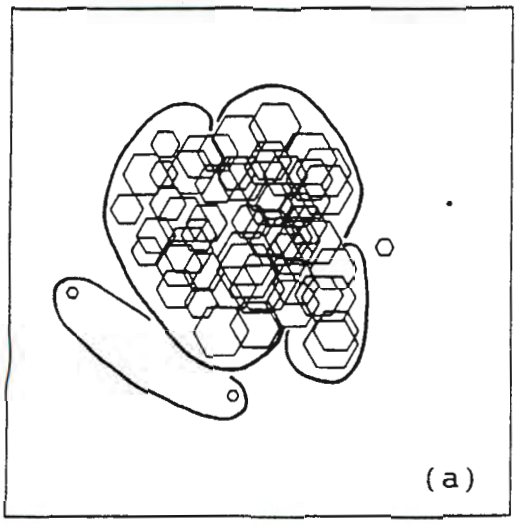
	Group A	Group B	Group C	Group D
Diversity	1.69±0.22	2.29±0.22	2.49±0.19	2.30±0.12
Evenness	0.39±0.05	0.53±0.04	0.57±0.04	0.53±0.02
Dominance	0.25±0.06	0.13±0.03	0.10±0.02	0.12±0.03
% scleractinia	63.2±9.41	60.7±16.1	66.5±16.9	56.2±5.85
% alcyonacea	27.6±8.38	37.4±15.1	32.3±15.5	43.7±5.85
% porifera	9.2±10.7	1.88±2.98	1.33±2.19	0
% others	0	0	0	0
%total living cover	79.9±6.96	77.5±11.5	65.8±12.7	66.2±14.9
%rock	20.1±6.69	22.1±10.9	31.7±15.4	31.3±10.6
%sand	0	0.36±1.84	2.52±9.76	0

Tab. 5: Summary statistics characterizing the clusters obtained in Fig.3. Values are mean and standard deviation.

venustum, Sinularia). This community was restricted to the peripheral areas of the flat, horizontal areas of the reef and gully edges (Fig.6d), with less coral coverage than the other groups ($\bar{x}$=66.2±7.44%, Fig.6a), more free rock ($\bar{x}$=31.3±5.31%, Fig.6b) but no resident sand (Fig.6c). It was the most diverse group ($\bar{x}$=2.49±0.05) with the highest evenness of species distribution ($\bar{x}$=0.57±0.011) and the lowest observed dominance ($\bar{x}$=0.10±0.006).

Group D was the most dissimilar group to all the other groups (Fig. 3), being very strongly soft-coral dominated (Tab.4). It was not as homogenous as the other groups (average similarity= 38.9%), which can also be seen by the fact that not all the transects in Group D clustered together in the MDS ordination. This was again a community of the flat, horizontal areas of the reef (Fig. 6d) with high coral coverage ($\bar{x}$=79.9±2.99%, Fig.6a), little unoccupied rock ($\bar{x}$=20.02±2.99%, Fig.5b) and no resident sand (Fig.6c). The diversity characteristics of group D were almost identical to those of group B, close to which it was found. High diversity ($\bar{x}$=2.30±0.06) and evenness ($\bar{x}$=0.53±0.01) were coupled with low dominance ($\bar{x}$=0.12±0.01).

The remaining transects, which did not fall within any distinct cluster, were all situated in gullies. They are loosely referred to as a "Gully-subcommunity". They had the highest dissimilarity to all other groups and were also very dissimilar to one another. All of them exhibited low coral coverage ($\bar{x}$=21.3±7.4%, Fig.6a), little free rock ($\bar{x}$=13.3±8.81%, Fig.6b), but high percentages of sand cover ($\bar{x}$=63.5±17.84, Fig.6c).

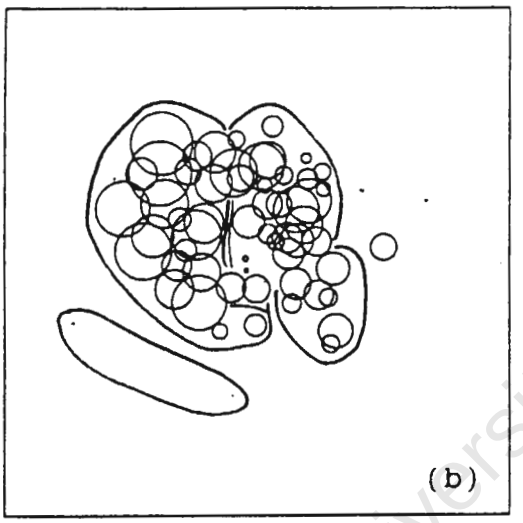


KEY
linear scale for proportional living coverage

20%

50%

80%

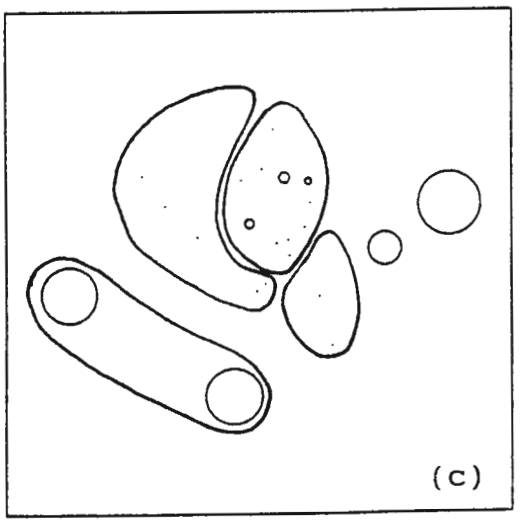


KEY
linear scale for proportion of unoccupied rock

20%

40%

60%

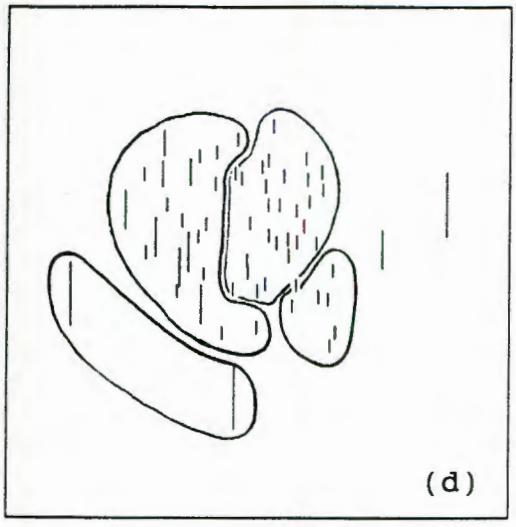


KEY
linear scale for proportion of sand

20%

40%

60%



KEY
linear scale for position of transects on the reef

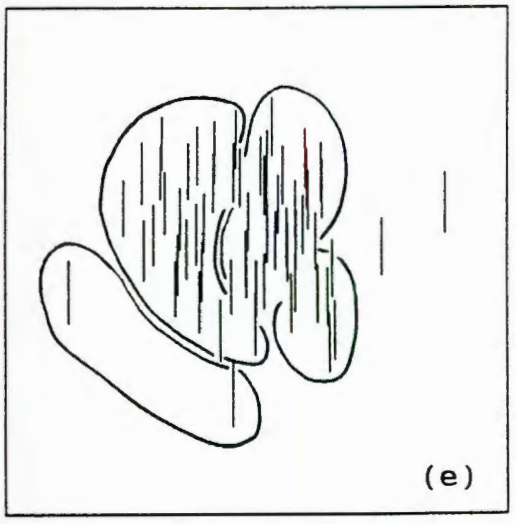
horizontal flat

ridge

gully edge

drop-off

inside gully



KEY
linear scale for depth of transects

20m

Fig. 6: Relation of transect groups to general community and substrate characteristics. The clusters in the MDS plots are the same as in Fig.5. At each sample point a) the hexagons are proportional in diameter to average coral coverage. b) Circles proportional in diameter to the proportion of unoccupied hard substratum. c) Circle diameter proportional to the proportion of sand in each transect. d) Relation of groups to topography: Each line length symbolizes a particular geomorphological area from which the samples were taken. e) line lengths indicate the depth of each sample.

All these subcommunities occupied the same depth range (between 18 and 24m). Depth therefore had no influence on coral community differentiation (Fig.6e).

All these subcommunities tended to intergrade to a certain extent. The distribution of the "Gully Subcommunity" was particularly ill-defined. Nevertheless, a typical pattern of Acropora dominated flat parts (either by branching A.austera or tabular A.clathrata), which intergraded with Sarcophyton dominated areas and markedly different edge and gully areas, dominated by Montipora and Lobophytum, emerged.

c) Within-community differentiation - the fossil dunes

While the deep outcrops generally lacked a depth stratification, this was not the case on the large fossil dunes forming 2-Mile Reef. The area covered by corals reached from about 8m (on the shallowest parts of the reefs) to about 40m depth.

The clusters shown in the dendrograms in Fig. 7 and the MDS plot in Figs. 8 were identical. Four groups of transects were found, three of which fell into distinct clusters, whilst the fourth group of transects did not form a homogeneous cluster.

A very distinct subcommunity was found (Cluster A) forming a well defined cluster, characterized by the highest dissimilarities to all other groups (Fig. 7). This subcommunity was not characterized by either hard or soft-corals but by sponges, sea fans of the genus Acabaria and various ascidians. Sponges were the dominant community members, occupying 20-70% of the total living coverage. Living cover in each transect was generally very low (18-28%). Also diversity was generally low ($\bar{x}$=1.59±0.33). This subcommunity was typically only found in depths greater than 25m (Fig.9e).

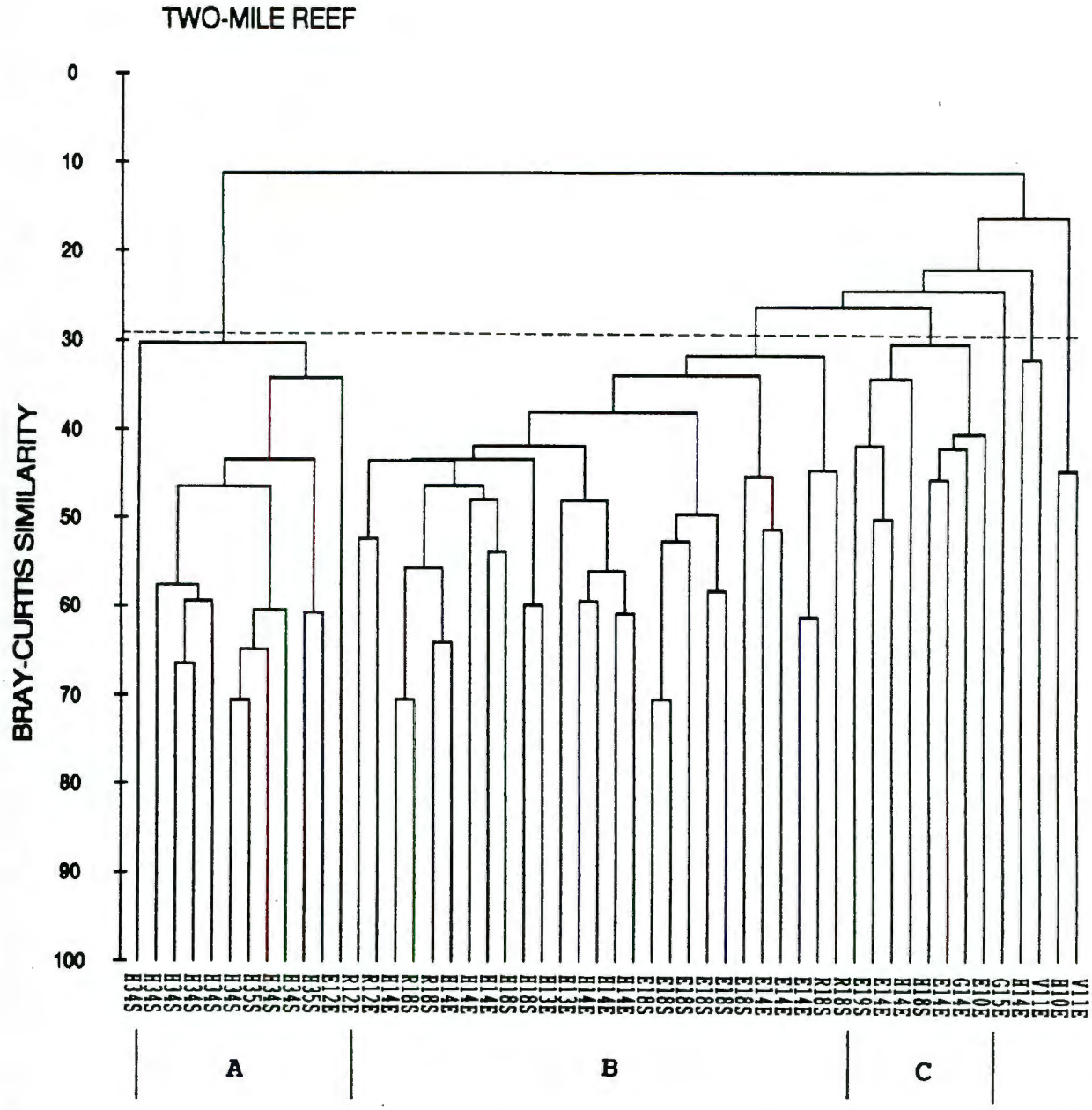


Fig. 7: Differentiation of the coral community on a typical fossil dune (2-Mile Reef) in the Central Reef Complex, as obtained by classification of root-root tansformed intercept data. Clustering algorithm was the same as in Fig.4. At an arbitrarily chosen distance of 29% similarity four main groups were distinguished, three of which were well grouped together and one very dissimilar to all others. Species responsible for within-group similarity and between-group dissimilarity are given in Table 5. Transects are coded to characterize their position on the reefs; R=Ridge, G=Gully, E=Edge, H=flat, horizontal area, the number gives the depth in metres; S=sheltered, E=exposed

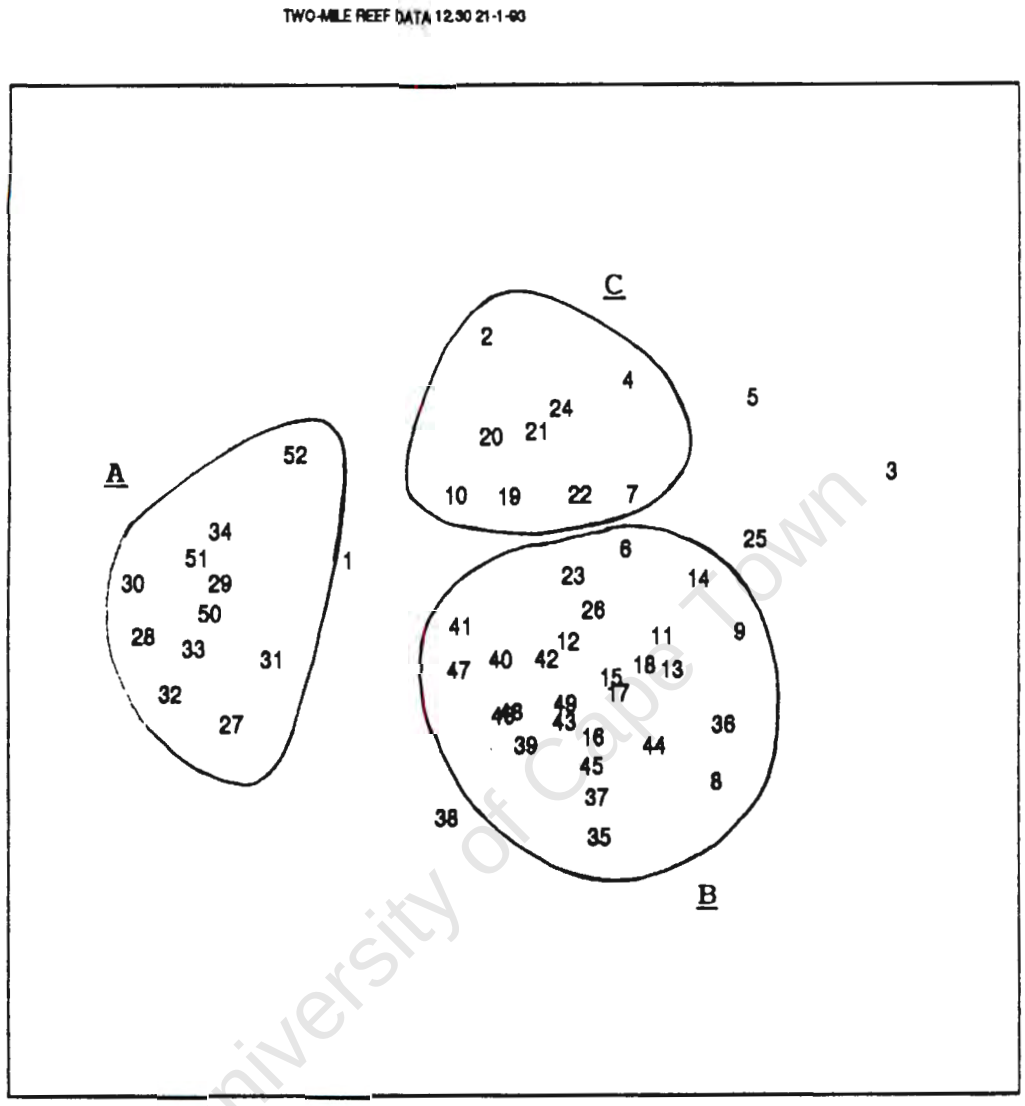


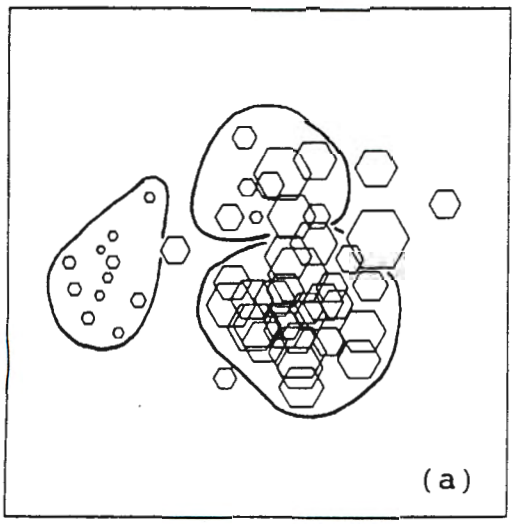
Fig. 8: Ordination of the 2-Mile Reef transects in 2 dimensions using multi-dimensional scaling on the same similarity matrix as Fig.7. The groups obtained by the dendrogram were superimposed onto the ordination plot by encircling each cluster of stations.

Average species dominance was low (x=0.35+0.10), which indicated a heterogenous community. Some hard corals, such as Podabacia crustacea and Diaseris distorta, were only recorded in this subcommunity. Other typical corals of the deep association were Coscinaraea monile and Oulophyllia crispa. Sea fans of the genus Acabaria as well as whip corals (Ellisella sp.) were common.

In depths less than 20m the coral community followed the differentiation of the substratum into flat areas and gullies as could be seen from the overlay of substratum characteristics over the MDS plot (Fig. 9). Cluster A comprised only transects from flat horizontal, deep areas with uniform, moderate percentage of sand on the substratum. Clusters B and C were from the shallower areas of the reefs, with less uniform percentage of sand but higher living coverage (Fig. 9a-e)

The most conspicuous grouping obtained from the Two-Mile Reef data, which was characterized by the biggest cluster at the arbitrary cut-off distance of 29%, was group B with an average within-group similarity of 31.1%. This cluster was dominated by the soft-coral genera Sinularia (amongst others, S. leptoclados and S. dura) and Lobophytum spp. (amongst others, L. venustum and L. patulum). Overall, Sinularia was the dominant genus. Space utilisation by hard and soft-corals did not differ significantly (t-test, $p<0.05$) and total living coverage was relatively low ($\bar{x}$=56.8±3.7%). The coral community recorded in these areas was amongst the most diverse encountered, with high average diversity ($\bar{x}$=2.11±0.06) and evenness values ($\bar{x}$=0.48±0.01) and low dominance ($\bar{x}$=0.17±0.01).

The third well-defined group (group C) included transects from gullies and gully-edges (Fig. 9d). Average Bray-Curtis similarity

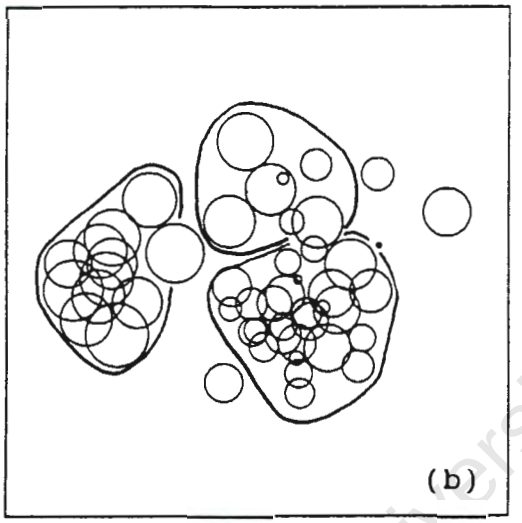


KEY
linear scale for proportional living coverage

20%

50%

80%

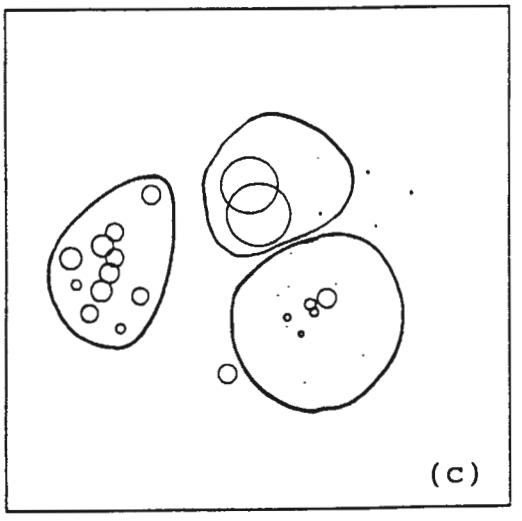


KEY
linear scale for proportion of unoccupied rock

20%

40%

60%

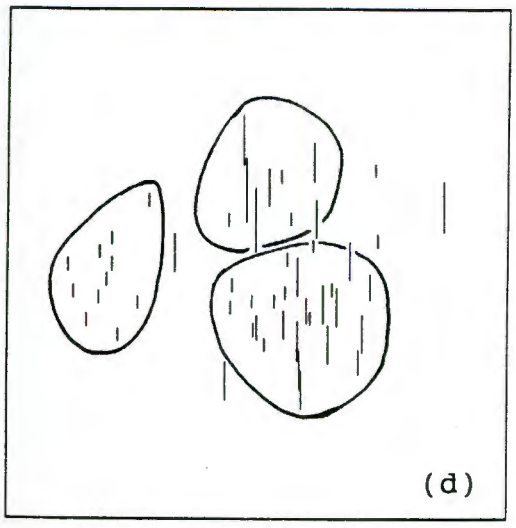


KEY
linear scale for proportion of sand

20%

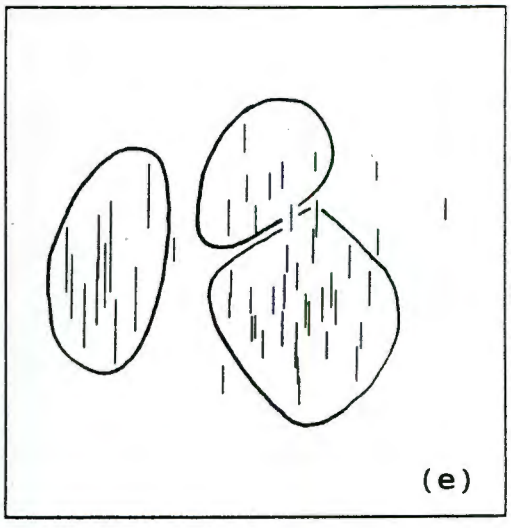
40%

60%



KEY
linear scale for position of transects on the reef

- horizontal flat
- ridge
- gully edge
- drop-off
- inside gully



KEY
linear scale for depth of transects

- 14m
- 20m
- 35m

Fig. 9: Relation of transect groups to general community and substrate characteristics. The clusters in the MDS plots are the same as in Fig.8. At each sample point a) the hexagons are proportional in diameter to average coral coverage. b) Circles proportional in diameter to the proportion of unoccupied hard substratum. c) Circle diameter proportional to the proportion of sand in each transect. d) Relation of groups to topography: Each line length symbolizes a particular geomorphological area from which the samples were taken. e) line lengths indicate the depth of each sample.

TWO-MILE REEF			
Group A		**Differences between groups A&B**	
1) Sponges	(36.4%)	1) Sinularia sp.2	(6.40%)
2) Gorgonians	(51.4%)	2) Sponge	(11.5%)
3) Ascidians	(62.5%)	3) Lobophytum venustum	(16.3%)
4) Podabacia crustacea	(72.2%)	4) Sinularia leptoclados	(20.8%)
5) Coscinaraea monile	(84.3%)	5) Sinularia dura	(24.5%)
Group B		**Differences between groups B&C**	
1) Sinularia gyrosa	(19.1%)	1) Montipora tuberculosa	(4.40%)
2) Lobophytum venustum	(30.1%)	2) Sinularia gyrosa	(8.68%)
3) Sinularia leptoclados	(46.7%)	3) Sinularia leptoclados	(12.8%)
4) Sinularia dura	(46.7%)	4) Lobophytum venustum	(16.5%)
5) Sarcophyton spp.	(54.4%)	5) Acropora clathrata	(20.2%)
Group C		**Differences between groups A&C**	
1) Lobophytum depressum	(16.4%)	1) Sponges	(6.14%)
2) Favites pentagona	(30.1%)	2) Montipora tuberculosa	(11.5%)
3) Montipora tuberculosa	(43.22)	3) Lobophytum depressum	(15.8%)
4) Sinularia gyrosa	(50.2%)	4) Sinularia gyrosa	(19.8%)
5) Favia favus	(56.8%)	5) Gorgonians	(23.3%)

Tab. 6: Species causing within-group similarity and between-group dissimilarity in the coral community on Two-Mile Reef. Species are listed in descending order according to their contribution to average Bray-Curtis similarity within groups or dissimilarity between groups. The numbers in brackets are cumulative values for contribution to average Bray-Curtis similarity or dissimilarity.

	Group A	Group B	Group C
Diversity	1.59±0.35	2.13±0.26	1.51±0.19
Evenness	0.37±0.08	0.49±0.05	0.35±0.04
Dominance	0.34±0.12	0.16±0.05	0.28±0.07
% scleractinia	40.5±24.8	55.3±17.7	33.3±4.90
% alcyonacea	14.3±8.44	44.4±18.1	28.0±30.8
% porifera	36.5±21.7	0	26.3±22.9
% others	7.60±6.87	0.28±0.75	12.3±18.0
%total living cover	23.4±15.6	55.6±15.6	43.6±9.71
%rock	59.6±13.9	32.5±9.33	56.3±9.71
%sand	17.5±10.1	16.9±22.6	0

Tab. 7: Summary statistics characterizing the clusters obtained in Fig.6. Values are mean and standard deviation.

within the group was 31.5%. Hard corals occupied significantly more space than soft corals (t-test, $p<0.05$), a clear dominance, however, was not observed. The dominant species were the soft corals Lobophytum patulum, L. depressum and Sinularia dura, which were typically encountered in gullies, and the hard corals Favites pentagona and Montipora tuberculosa. All these species were also typical in the "gully-cluster" on Four-Mile Reef. The group was characterized by relatively low coral coverage ($\bar{x}$=55.8±5.9%, Fig.8a), a high percentage of free rock ($\bar{x}$=32.5±3.5%, Fig.9b) and the highest percentage of sand ($\bar{x}$=16.9±8.5%, Fig.9c) in any subcommunity on Two-Mile Reef. Within sandy gullies corals were limited to the often strongly sloping or near vertical walls or to hard substratum projecting above the sand. The diversity was very high ($\bar{x}$=02.13±0.09), as was the evenness of species contribution ($\bar{x}$=0.49±0.02). Dominance within this subcommunity was the lowest observed on Two-Mile Reef ($\bar{x}$=0.16±0.02).

The "Sinularia reef-top" subcommunity and the "gully" subcommunity shared the same depth range (8-14m). The "gully-subcommunity" occupied less space on the substratum due to its confinement to gullies.

The community was thus divisible into a shallow "reef-top subcommunity" (dominated by soft corals of the genera Sinularia and Lobophytum), a "gully-subcommunity" (dominated by soft co rals of the genus Lobophytum and hard corals of the genera Montipora and Favites) and a "deep-reef subcommunity" in depths greater than 25m (dominated by sponges, ascidians and sea-fans).

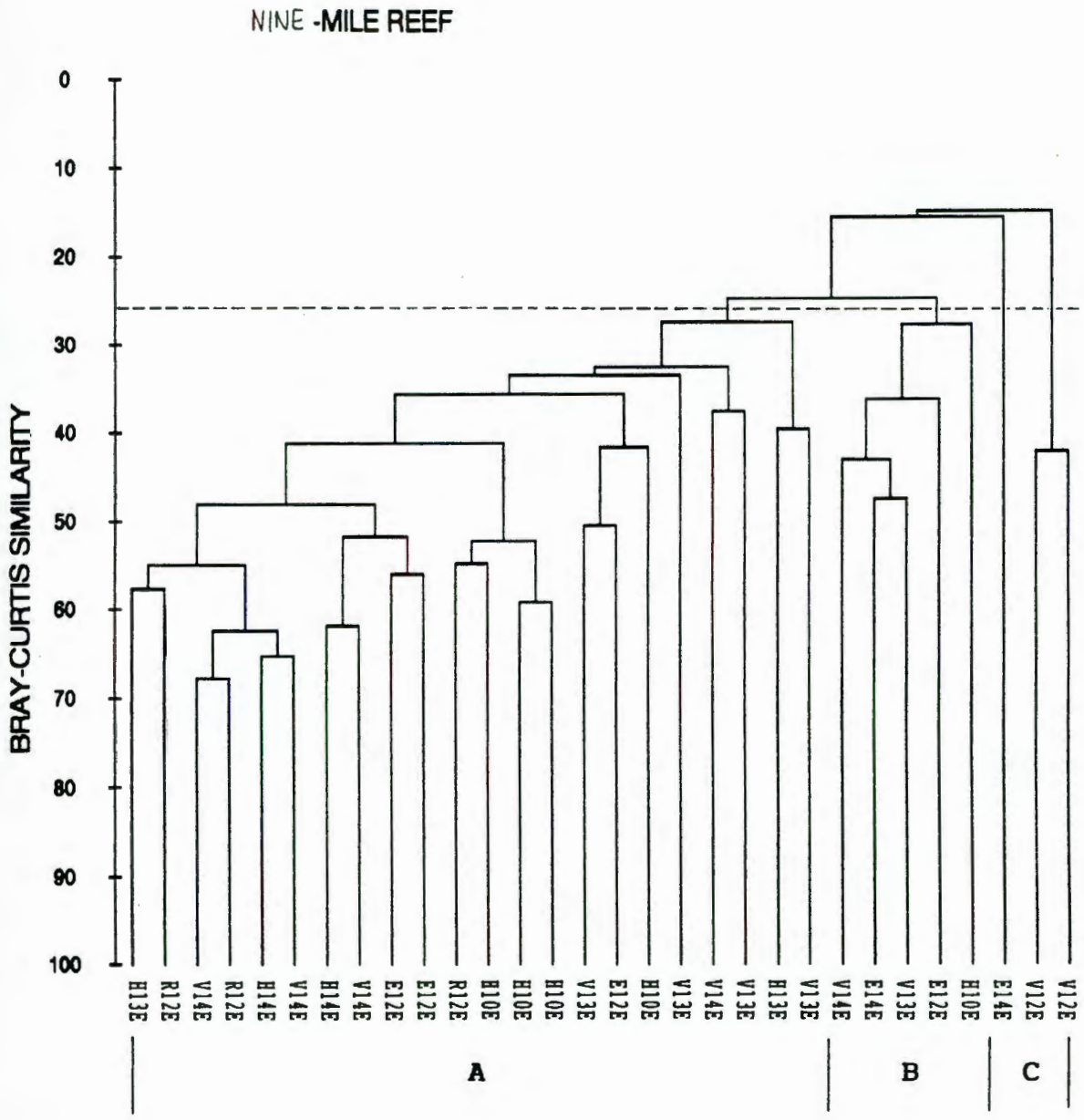


Fig.10: Differentiation of the coral community on a fossil beach-rock platform (9-Mile Reef) in the Central Reef Complex, as obtained by classification of root-root transformed intercept transect data. Clustering algorithm was the same as in the other analyses. At an arbitrary cut-off distance of 26%, 3 groups were formed, of which only two were well defined. Species responsible for within group similarity and between group dissimilarity are given in Table 7. Transects are coded to characterize their position on the reefs; R=Ridge, V=Drop-off, E=Edge, H=flat, horizontal area; the number gives the depth in metres; E=exposed.

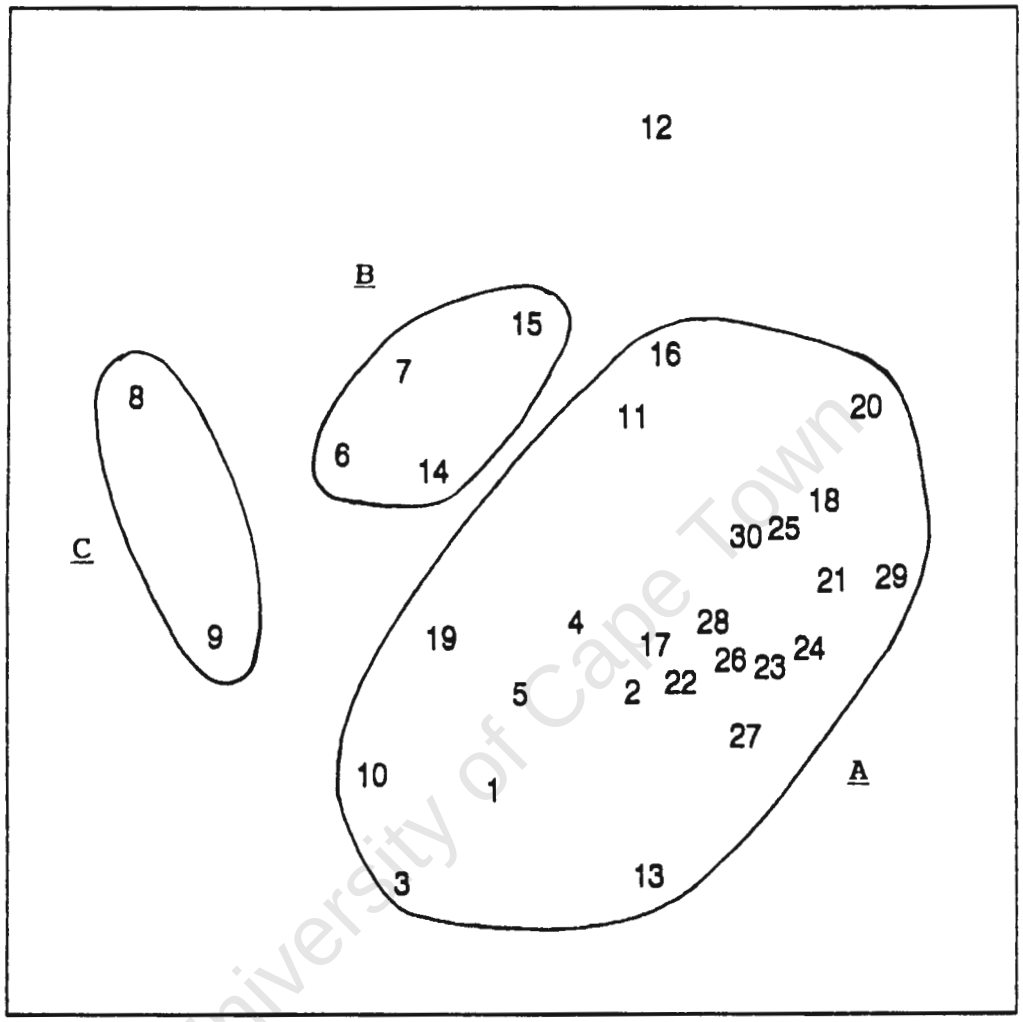


Fig.11: Ordination of the 9-Mile Reef transects in 2 dimensions using multi-dimensional scaling on the same similarity matrix as Fig.10. The groups obtained by the dendrogram were superimposed onto the ordination plot by encircling each cluster of stations.

NINE-MILE REEF			
Group A		**Differences between groups A&B**	
1) Lobophytum sp.4	(21.2%)	1) Lobophytum sp.4	(6.30%)
2) Sinularia gyrosa	(41.5%)	2) Sinularia gyrosa	(11.7%)
3) Lobophytum depressum	(52.3%)	3) Acropora clathrata	(16.6%)
4) Lobophytum venustum	(59.6%)	4) Porites lichen	(21.4%)
5) Sarcophytum spp.	(65.5%)	5) Hydnophora microconos	(24.8%)
Group B		**Differences between groups B&C**	
1) Acropora clathrata	(19.4%)	1) Sponges	(9.55%)
2) Porites lichen	(37.6%)	2) Ascidians	(16.4%)
3) Favites pentagona	(53.3%)	3) Porites lichen	(21.9%)
4) Acanthastrea echinata	(61.8%)	4) Lobophytum venustum	(26.1%)
5) Lobophytum venustum	(69.4%)	5) Lobophytum depressum	(30.1%)
Group C		**Differences between groups A&C**	
1) Sponges		1) Sinularia gyrosa	(6.92%)
2) Ascidians		2) Sponges	(13.8%)
3) Lobophytum depressum		3) Lobophytum sp.4	(20.5%)
4) Acropora clathrata		4) Ascidians	(27.2%)
5) Pocillopora verrucosa		5) Pocillopora verrucosa	(32.9%)

Tab. 8: Species causing within group similarity and between group dissimilarity in the coral community on Nine-Mile Reef. Species are listed in descending order according to their contribution to average Bray-Curtis similarity within groups or dissimilarity between groups. The numbers in brackets are cumulative values for contribution to average Bray-Curtis similarity or dissimilarity. No cumulative similarity statistics are given for group three, as it comprised only two transects, which did not allow computation of statistics. Species given are those with highest proportional share in the subcommunity.

d) Within-community differentiation - the submerged beach rock platforms

Although not seperable from Red-Sands and Two-Mile Reefs in the initial ordination (Fig.3), Nine-Mile Reef exhibited a different morphology to these fossil dunes and to the deep outcrops, and was therefore also evaluated seperately. According to Ramsey & Mason (1990) Nine-Mile Reef is a fossil beach rock platform. It extends from about 6m depth at its shallowest point to 18m at its base. Topographically it comprises a wide, flat platform (at an average depth of 12m), dissected by numerous gullies and forming drop-offs in some areas at its edge (between 12 and 18m).

In this coral community soft corals occupied significantly more space than hard corals (t-test, $p<0.05$, Tab.2), the overall average diversity of all samples obtained from this reef was low ($H'=2.01\pm0.33$), having the same value as the average of the total community on 2-Mile Reef including the depauperate deep area.

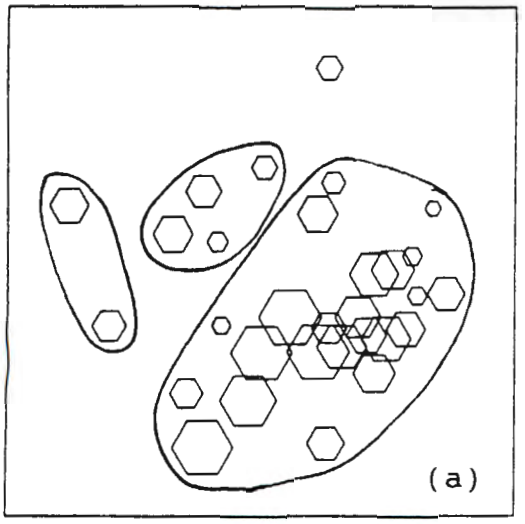
Similar to the situation on the other reefs the differentiation in this community followed the topography and divided into "top" and "gully" subcommunities (Fig.10, Fig.12d).

The transects within the "gully groups" were very dissimilar, not all falling within a single cluster. They lacked a characteristic set of dominant species, a situation already observed on the other reefs.

Group B, which comprised transects from gullies and gully edges (Fig.12e), had an average within-group similarity of 39.6% and was dominated by hard corals (Acropora clathrata, Porites lichen, Favites pentagona, Acanthastrea echinata). It was characterized by relatively high living cover ($\bar{x}=56.7\pm6.26\%$, Fig.12a), large amounts of free rock ($\bar{x}=43.2\pm6.2\%$, Fig.12b) but no sand (Fig.12c).

	Group A	Group B	Group C
Diversity	2.04±0.29	2.28±0.31	1.51±0.19
Evenness	0.47±0.06	0.52±0.07	0.35±0.04
Dominance	0.17±0.05	0.13±0.06	0.28±0.07
% scleractinia	30.7±17.8	76.5±21.8	33.3±4.90
% alcyonacea	65.1±21.2	23.5±21.8	28.0±30.8
% porifera	4.16±7.18	0	26.3±22.9
% others	0.1±0.47	0	12.3±18.0
%total living cover	60.4±19.1	56.7±12.5	43.6±9.71
%rock	39.8±18.7	43.2±12.4	56.3±9.71
%sand	0	0	0

Tab. 9: Summary statistics characterizing the clusters obtained in Fig.9. Values are mean and standard deviation.

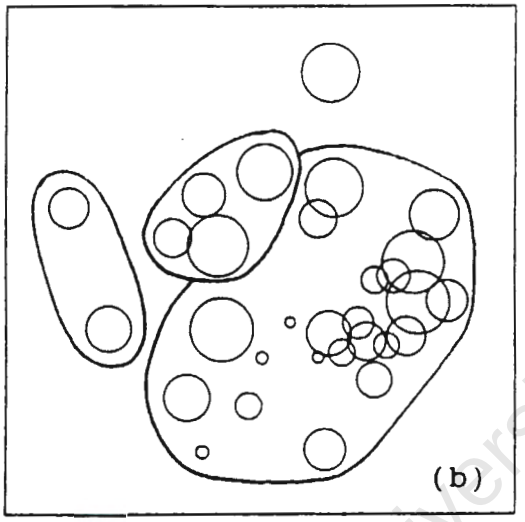


KEY
linear scale for proportional living coverage

20%

50%

80%

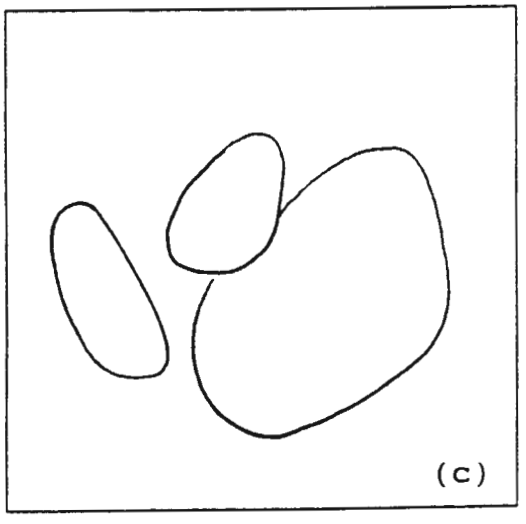


KEY
linear scale for proportion of unoccupied rock

20%

40%

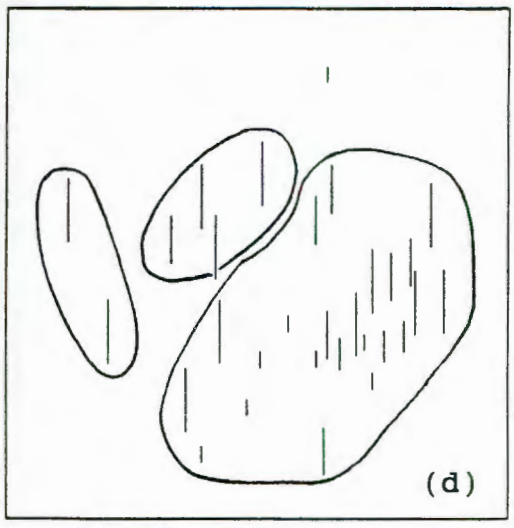
60%



KEY
linear scale for proportion of sand

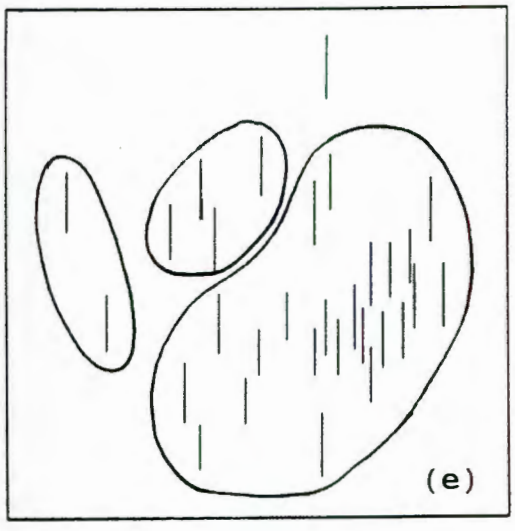
all transects

with 0% sand



KEY
linear scale for position of transects on the reef

- horizontal flat
- ridge
- gully edge
- drop-off
- inside gully



KEY
linear scale for depth of transects

- 14m
- 20m
- 35m

Fig.12: Relation of transect groups to general community and substrate characteristics. The clusters in the MDS plots are the same as in Fig.11. At each sample point a) the hexagons are proportional in diameter to average coral coverage. b) Circles proportional in diameter to the proportion of unoccupied hard substratum. c) Circle diameter proportional to the proportion of sand in each transect. d) Relation of groups to topography: Each line length symbolizes a particular geomorphological area from which the samples were taken. e) line lengths indicate the depth of each sample.

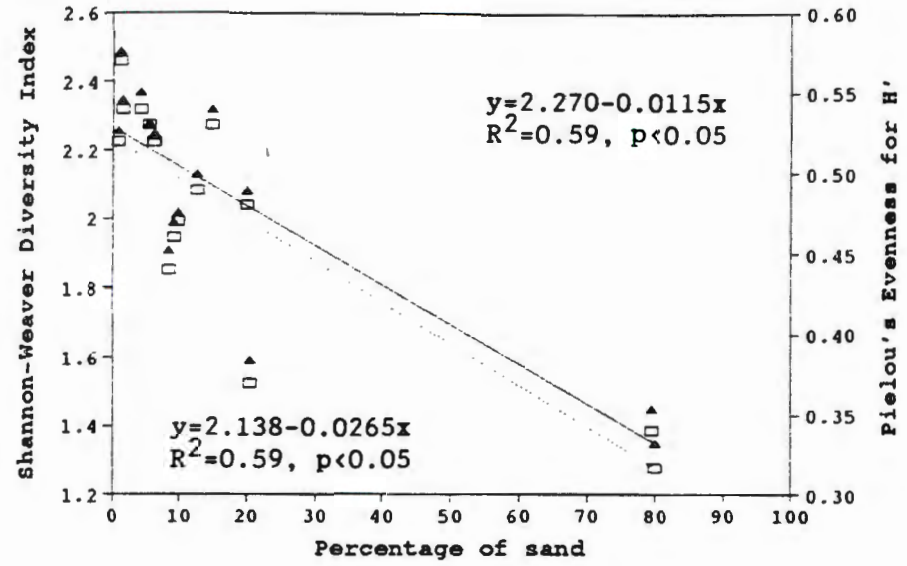
Diversity was high ($\bar{x}$=2.28±0.15) with a high eveness of species contribution ($\bar{x}$=0.52±0.03) and low dominance values ($\bar{x}$=0.13±0.03). The biggest cluster, group A, with an average within-group similarity of 38.4%, was strongly soft-coral dominated, Lobophytum and Sinularia being the most important genera. The transects within this group were from flat, horizontal parts of the reef, from edges and drop-offs (Fig.12e) and were characterized by higher living coverage than in the other groups ($\bar{x}$=60.4±39.8%, Fig.12a), but also a relatively high average proportion of unoccupied rock, although with high variability ($\bar{x}$=39.8±4.4%, Fig.12b) and no sand (Fig.12c). Diversity was lower than in the gullies ($\bar{x}$=2.04±0.06), as was evenness ($\bar{x}$=0.47±0.01) but dominance was higher ($\bar{x}$=0.17±0.01).

The sub-communities found on the beach-rock outcrops were very similar to those found on the fossil dunes.

e) General community characteristics

As could be seen from the overlay plots on the MDS ordinations (Figs.6,9,12a-e), the substratum characteristics with the strongest influence on community structure were (a) the location of the samples (whether they were on flat areas or in gullies) and (b) depth, with a strong differentiation along a depth gradient. Proportion of sand within the community was generally closely linked to the location of the samples, being highest in the gullies.

A significantly negative relationship was found between the percentage of sand within a community and its diversity ($r=-0.77$, $p<0.05$), and evenness ($r=-0.77$, $p<0.05$, Fig.13 a). A positive relationship existed between the dominance index and the



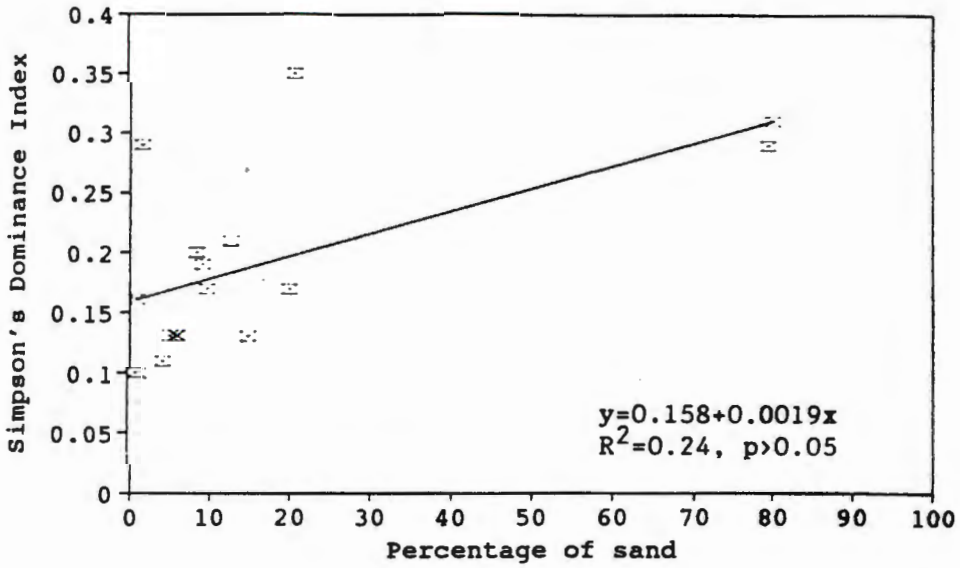


Fig.13 a,b: Correlation between the percentage of sand in the substratum within the subcommunities on all rees and a) Shannon-Weaver diversity (dotted line and open squares) and evenness (solid lines and full triangles) b) Simpson's dominance index.

percentage of sand in the communities, which, however, was not significant (r=0.47, p=0.07, Fig.13b). Diversity was significantly lower at depths of less than 18m than in the grouping 18-25m. It then declined significantly again on the deep reef community (ANOVA, F=6.27, df:3,50, p=0.001).

Maximum measured sedimentation levels in the gullies were 1.8kg $m^{-2}hr^{-1}$ in gullies and 0.7kg $m^{-2}hr^{-1}$ on the elevated parts. Maximum measured levels of sediment suspended in the watercolumn was 0.4gl^{-1} in the gullies and 0.1gl^{-1} on the elevated parts. Both sedimentation rates and levels of suspended sediment in the watercolumn were significantly higher in the gullies than on the elevated parts of the substratum (t-tests, $p<0.001$, $p<0.05$).

Discussion

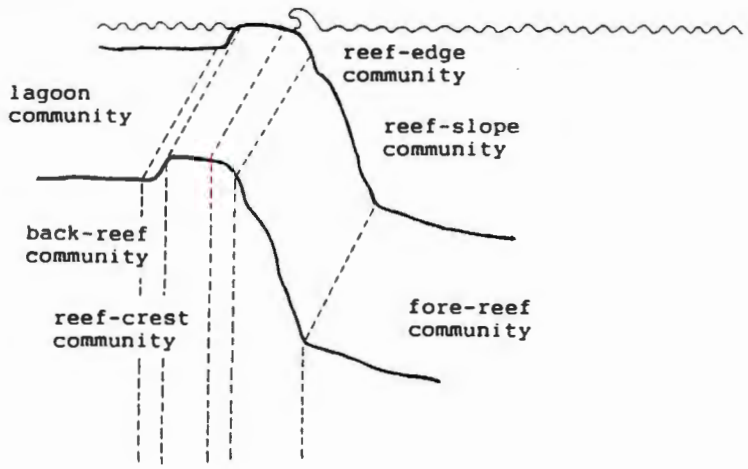
Even though situated in a very southerly location, the South African coral communities are very rich, both in species richness and in coral coverage of the substratum. There was, however, a gradient in species richness from North to South. While the coral species are typical for the Indo-Pacific reef belt (Sheppard, 1987), the South African reef systems themselves deviate markedly from the usual situation on most other coral reefs (Fig. 12). The substratum underlying the coral communities in South Africa is not that of a typical coral reef and no signs of active reef accretion were evident. They seem to be reef coral communities, composed of typically hermatypic species, which nevertheless are not building reefs. Therefore most of the morphological features typical of true coral reefs are missing. The area is very flat and offers a relatively uniform environment as changes in depth occur along a very mild gradient. Over wide areas the substratum is not

structurally complex. Despite this, the results of the present study show clearly that there is a differentiation into distinct subcommunities.

The coral communities seemed to differentiate primarily along the axes of depth and sedimentation (higher sedimentation rates in the gullies were inferred by the higher proportion of sand on the substratum and also measured in the field), as could clearly be seen by the community's reaction to these parameters. Depth also had important implications for water motion and light, which obviously decreases with depth. Sedimentation is also strongly linked to depth and water motion, as strong water movement can resuspend resident sediment. Almost all the sedimentation observed within the Central and Southern Reef Complexes was caused by resuspension of resident, biogenic sediments as there are no rivers importing any allochthonous sediments in this region. The morphology of the substratum played an important role. Strong sedimentation was not observed on the elevated parts of the reefs, where hardly any resident sediment was found. It was concentrated within the gullies, where water movement was channeled due to surge and was able to move the sand which had naturally accumulated within these depressions.

Therefore, a very clear differentiation of the coral communities occurred between high-sedimentation areas (e.g. gullies) and low-sedimentation areas such as high-lying flat areas and ridges (Fig.2). Low sedimentation "reef-top sub-communities" were always dominated by a specific group of soft-corals (belonging to the genera Lobophyton and Sinularia), while the high sedimentation "gully sub-communities" were mostly hard coral dominated, but very heterogeneous, without a specific set of dominant species. I

a) typical coral reef



b) South African reef systems

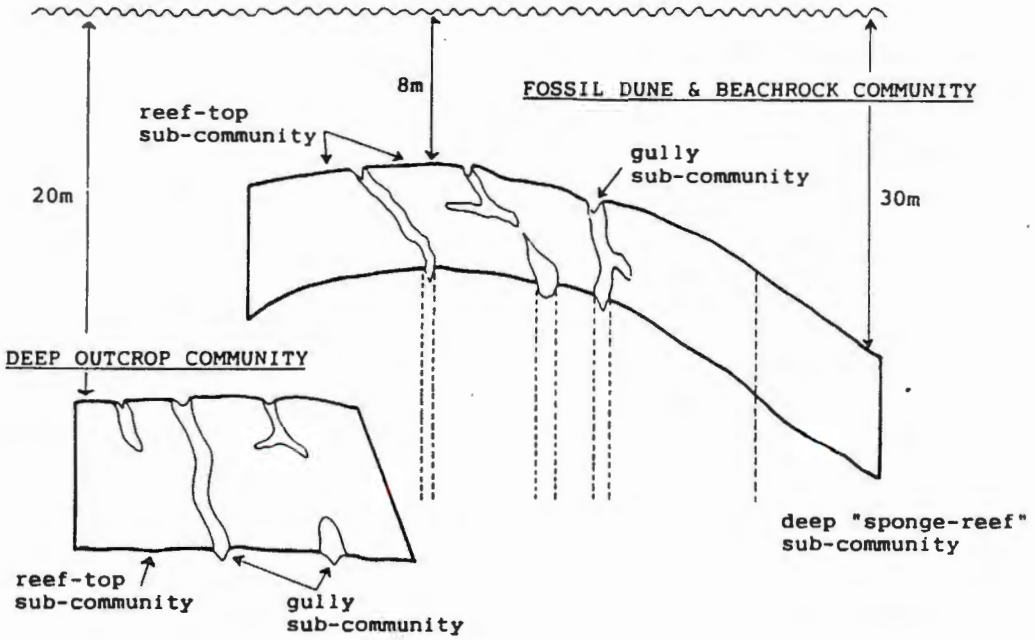


Fig.14: Idealized diagrams illustrating the main differences between South African reef systems and typical coral reefs. Depths in Fig.b are not to scale. The community differentiation in Fig. a) is a generalization condensed from reports in the literature (e.g. Loya, 1972; Sheppard, 1982; Done, 1982).

hypothesize that the observed preference of soft corals for elevated areas with comparatively little sedimentation is due to their being relatively intolerant of long-term sedimentation. The lower diversity in gullies and areas subjected to high sedimentation suggest that only a limited number of species are able to cope with such conditions. Similar suggestions have been made by Dai (1991) to explain coral community structure in Taiwan. These assumptions will be experimentally tested in Chapter III.

The general dominance of soft corals, exept in adverse environments, can possibly be explained by their having a faster growth rate than hard corals which may also result in bigger colonies. However data to affirm this assumption are not available.

Except on the deep reef, where corals did not dominate the community, light did not seem to have a significant influence on corals. This seemed to hold true at least for coral coverage and average colony size, both of which were higher on the outcrops at around 20m depth than on the shallower areas of the fossil dunes and beachrock outcrops. This suggests that these corals have to be shade-adapted, a possibility that is explored in experiments in Part III.

In other areas, like the Great Barrier Reef (Potts et. al., 1984) and the Red Sea (Riegl & Velimirov, unpubl.data) coral size often increases up to a certain depth ("deep water gigantism", Hughes, 1984). One of the reasons why colony size increases in deeper water could be the relatively greater shelter there from wave-created surge-action. The South African reefs are exposed to open ocean swells. This situation was particularly well illustrated by the distribution of the hard coral genus Acropora on the reefs. The only areas in which they dominated were in depths greater than

20m. There, Acropora austera formed large, open arborescent colonies and the tabular A. clathrata dominated wide areas of reef. It is likely that these species would be unable to survive on the shallower reefs as their shape would induce high drag and cause structural failure during storms. The dominant corals in the shallow areas are therefore massive (eg. Faviidae), low branching (Pocilloporidae) or leathery (soft-corals). Most massive corals grow hemispherically, which is an advantageous growth form in situations of high water movement (Vogel, 1981). In addition, A. austera seems to be very proficient at asexual reproduction by fragmentation (see Part III). It seems unlikely that fragments would have much chance of survival in areas of high surge on the shallow reefs. Both the shape and the reproductive mode of A.austera do not seem to be adapted to a high surge environment, which would explain its being common in deeper areas only. Experiments in Part III will clarify this point.

According to Dai (1991), soft corals suffer more heavily under storm seas than hard corals in Taiwan. I did not observe a similar situation in South Africa, where soft corals dominated the very areas subjected to highest surge.

Some of the observed subcommunities coexist within the same depth range and a fair amount of overlap exists. The relative uniformity of the reef's bathymetry also caused each community type to be repeatedly realized within its depth zone. Both in the shallow and the deep areas it was very apparent that gullies with "gully-subcommunities" repeatedly alternated with elevated parts of the substratum supporting "top-subcommunities".

Conclusion

South African coral communities, which are made up mostly of typically Indo-Pacific coral species but do not form typical coral reefs and appear to be differentiated by the environmental parameters of water motion, sedimentation and light. The community structure can possibly be explained by the varying ability of hard- and soft coral species to withstand sedimentation stress and strong water movement. Strong wave action and sedimentation on the shallow reefs shaped a coral community different from than on the deep reefs, where water movement is less important. Soft corals dominated the areas of low sediment stress on the shallow reefs, while hard corals with mostly massive growth form dominated the gullies, areas of high sedimentation. Branching and tabular species of hard coral were dominant on the deep reefs only, seemingly excluded from dominance in the shallower areas by strong water movement. In the deepest areas of the reefs, hard and soft corals became very rare, possibly excluded by lack of light. The deep communities were dominated by sponges, sea fans and ascidians, which do not rely on light in order to meet their energetic requirements.

Literature cited

Benayahu, Y. in press. Alcyonacea from Sodwana Bay, South Africa. Invest. Rep. Oceanogr. Res. Inst., Durban (67): 1-15.

Boshoff, P. (1980). The corals of Maputaland. in:Bruton, M. & K.H. Cooper (eds.): Studies on the ecology of Maputaland. Rhodes University, Grahamstown and WSSA, Durban: 8-11.

Brower, J.E. & J.H. Zar (1977). Field and laboratory techniques for general ecology. Wm.C.Brown, Dubuque, Iowa: 1-315.

Clarke, K.R & R. M. Warwick. pers. comm. Statistical analysis and interpretation of marine community data. IOC Manuals and Guides No.22, Plymouth Marine Laboratory, UK.

Dai, C.F. (1991). Distribution and adaptive strategies of alcyonacean corals in Nanwan Bay, Taiwan. Hydrobiologia 216/217: 241-246.

Digby, P.E. & R.E. Kempton (1987). Multivariate analysis of ecological communities. Chapman & Hall, London: 1-206.

Dinesen, Z.D. (1983). Patterns in the distribution of soft-corals accross the Great Barrier Reef. Coral Reefs 1: 229-236.

Done, T.C. (1982). Patterns in the distribution of coral communities accross the central Great Barrier Reef. Coral Reefs 1(1): 95-107.

Field, J.G., K.R. Clarke & R.M. Warwick (1982). A practical ategy for analysing multispecies distribution patterns. Mar.Ecol.Progr.Ser. 8: 37-52.

Highsmith, R.C. (1982). Reproduction by fragmentation in corals. Mar.Ecol.Progr.Ser. 7: 207-226.

Hubbard, D.K. (1986). Sedimentation as a control of reef development: St.Croix, USVI. Coral Reefs 5: 117-125.

Hughes, T.P. (1984). Population dynamics based on indivual size rather than age: ageneral model with a reef coral example. Amer.Nat. 123: 81-101.

Loya, Y. (1972). Community structure and species siversity of hermatypic corals at Eilat, Red Sea. Mar.Biol. 13(2): 100-123.

Loya, Y. (1978). Plotless and transect methods. in: Stoddart, D.R & R.E. Johannes (eds.): Coral reef research methods. UNESCO, Paris: 581-591.

Pielou, E.C. (1975). Ecological diversity. Wiley, New York.

Potts, D.C., T.J. Done, P.J. Isdale & D.A. Fisk (1985). Dominance of a coral community by the genus Porites (Scleractinia). Mar. Ecol.Progr.Ser. 23: 79-84.

Ramsey, P.J. & T.R. Mason (1990). Development of a type zoning model for Zululand coral reefs, Sodwana Bay, RSA. J,Coastal Res. 6(4): 829-852.

Rogers, C.S. (1990). Responses of coral reefs and reef organisms to sedimentation. Mar.Ecol.Progr.Ser. 62: 185-202.

Schumann, E.R. & M.J. Orren (1980). The physico-chemical characteristics of the South West Indian Ocean in relation to Maputaland. in:Bruton, M. & K.H. Cooper (eds.): Studies on the ecology of Maputaland. Rhodes University, Grahamstown and WSSA, Durban: 8-11.

Sheppard, C.R.C. (1981). The groove and spur structures of Chagos Atoll and their coral zonation. Estuarine, Coastal & Shelf Science 12: 549-560.

Sheppard, C.R.C. (1982). Coral populations on reef slopes and their major controls. Mar.Ecol.Progr.Ser. 7: 83-115.

Sheppard, C.R.C. (1987). Coral species of zhe Indian Ocean and adjacent seas: a synonymized compilation and some regional distribution patterns. Atoll Research Bulletin 307: 1-32.

Stoddart, D.R. (1969). Ecology and Morphology of recent coral reefs. Biol.Rev. 44: 433-497.

Veron, J.E.N. (1986). Corals of Australia and the Indo-Pacific. Angus & Robertson, North Ryde.

Vogel, S. (1981). Life in moving fluids. Princeton University Press.

P A R T III

The Processes: Experimental testing of the formulated hypotheses

In this third part of the thesis I subject some of the hypotheses formulated in the previous parts to experimental testing. In particular the hypotheses that the coral communities are primarily influenced by wave-action and sedimentation. These two aspects are investigated in a series of experiments.

COLONY SIZE AND FRAGMENT SURVIVAL OF THE BRANCHING CORAL *ACROPORA AUSTERA* (Anthozoa:Scleractinia) IN RELATION TO WAVE ACTION IN A MARGINAL HABITAT

Abstract

The influence of wave action on colony size and shape and on the survival of fragments of the branching coral *Acropora austera* was investigated experimentally *in situ* on South African reefs and in the laboratory. Size and shape of entire colonies as well as the numbers of unattached fragments were recorded as a function of depth. Colonies had long, easily broken branches only in depths greater than 18m. Experimental breakage was inflicted on colonies experiencing varying degrees of wave-exposure and the survival of these fragments, through time, was monitored. A clear positive correlation existed between depth, recovery rates of fragments and overall survival. The most important morphometric parameters enhancing tissue-survival of fragments were the number of tips, the maximum width, the area of surface contact and the volume of space occupied by the fragment. In the first month all small fragments died, leading to very uniform size and shape of fragments surviving longer than one month. Skeletal recovery was slow, at the rate of 1.25 mm per month. A "shape-dependent survivorship" hypothesis for coral fragments is proposed.

Introduction

In Part II of this thesis I established that differences exist in community structure between the shallow and the deep reefs in South Africa, the deep areas being dominated by either tabular or branching Acropora species, such as A. austera. I speculated that wave action may be an important factor influencing this differentiation, because it may prevent branching and easily fragmented species from becoming dominant in shallow areas by interfering with their fitness. Theoretically, this could be achieved either by breakage of colonies or by making it impossible to reproduce asexually. Asexual reproduction is known to be an important means of propagation in many branching corals and allows them to quickly monopolize large areas of reef (Highsmith, 1982; Wallace, 1985). This chapter sets out to test the effects of wave action on breakage and asexual reproduction by fragmentation.

The breakage of corals on reefs is a well documented and common occurrence, which can either occur accidentally, through high water movement or direct human interference (Mah & Stearn, 1986; Riegl & Velimirov, 1991), or it may be caused by the corals themselves (Highsmith, 1982; DeVantier & Endean, 1989). Breakage occurs most commonly in branching corals (Tunnicliffe, 1981; Riegl & Velimirov, 1991). A number of coral species are able to turn the apparent disadvantage of losing part of the colony into a means of asexual reproduction (Highsmith, 1982; Wallace, 1985), however, high mortalities may follow relocation of the fragments (Yap et al., 1992).

While the phenomenon of fragmentation is well described (Loya, 1976; Tunnicliffe, 1981; Chadwick & Loya, 1991), more work is needed to investigate the survival of individual fragments. Also,

while the size of the fragments has received attention and was found to be linked to survival (Loya, 1976; Highsmith et al., 1980; Hughes, 1989; Lewis, 1991), the importance of the overall shape of the fragments has mostly been overlooked. One such study exists for a fungiid coral (Chadwick & Loya, 1991).

South African coral communities live in a marginal environment, both geographically and environmentally. They live at the southernmost limit of the distribution of many of the constituent species and the environment is characterized by strong water movement (see Part II). The question arose as to whether successful asexual reproduction by fragmentation is possible under these circumstances. It seems likely that survival of fragments in such a habitat might depend on their shape, which could produce different reactions to the physical environment. The coral species used in the experiment (Acropora austera) is one of the most common branching coral species found in South African coral communities.

As the central question is, whether wave action is forcing the community structure of South African coral communities, the reaction of entire colonies and of fragments derived from them to different wave exposure was investigated.This chapter examines: 1) the size and shape of colonies in different depth and therefore wave exposure and the influence of colony shape on fragmentation. 2) the correlation between survival of Acropora austera fragments and their size and shape. I set out to investigate the hypothesis that fragment shape is a determining factor in fragment survival; 3) a comparison between different environments on the reefs.

Material and Methods

For the experiments, five sites within three depth ranges were chosen - one site at 12m depth on 2-Mile Reef (consisting of two sub-sites, one in a gully and one on a ridge), one site at 18m on 4-Mile Reef, and another site at 21m on 4-Mile Reef, which consisted of three sub-sites. The shallow (12m) site was situated on 2-Mile Reef because the shallowest areas supporting corals on 4-Mile Reef are at 18m depth and one of the questions was why A. austera was not common on shallow reefs such as 2-Mile Reef. 4-Mile Reef is a very flat sand-stone outcrop. The four sites chosen there represent all major environments on this reef and differed in substratum type, morphology and coral cover. Site one (18m) was situated on a very gentle slope on the edge of the reef, site two (21m) was a shallow depression on the reef with no coral cover within it but rich coral cover around it, site three (21m) was situated on the lower edge of a ledge, site four (21m) was on a flat sand plain, 1m from the edge of the reef. These sites also represent environments of different wave exposure, as water movement due to wave-action decreases with depth (Denny, 1988), sites in greater depth represent sites of lesser wave exposure.

A. austera occurs from 10-25m depth, but is most abundant and forms the largest colonies in a depth range between 18 and 24m on Maputaland reefs. Therefore, emphasis was placed on sampling and experimenting in this depth. In depths shallower than 18m, A. austera is generally uncommon and small, or does not occur at all over wide areas of the reefs. For more information on coral community structure at the sites see Part II.

The fragments used for the survival experiment at the 12m depth site on 2-Mile Reef were taken from colonies at 21m depth on 4-

Mile Reef and transplanted, as A. austera is rare on 2-Mile Reef. The fragments for all other sites were derived from colonies growing in the immediate vicinity of the experimental area. A total of 170 fragments was used at the 5 sites.

After one month, the fragments were collected and analyzed. The percentages of fragments recovered from each site were recorded. They were then grouped into five categories consisting of specimens with 100%, up to 75%, up to 50%, up to 25% and 0% surviving soft tissues. Surviving soft tissues were easily identified by their cream to yellow colour. No bleaching, which would have made tissue recognition difficult, was observed.

For each fragment, measurements were made of fragment length, width, height, and the number of tips within the fragment (eg. the number of branchlets) were taken (Fig. 1). As an index of volume occupied by the fragment, each fragment was considered as a pyramid, the basal area of which was calculated as illustrated in Figure 2 and the height of which was given by the length of the fragment. The assumption that the fragments occupied a roughly pyramidal space held true in most cases. An index of the area of contact with the substratum was calculated as a triangle given by the fragment's greatest length and width (Fig. 1).

Because of low recovery rates it proved impractical to leave fragments on the reef for longer than one month. Tests of further survival were therefore undertaken in an aquarium at the Oceanographic Research Institute in Durban. Fragments were transported to the aquarium by truck in a 500 litre container with sea water slightly hypersaturated with medical oxygen. During transportation the fragments were not allowed to become dry or to come into contact with air for longer than 5 sec. In the aquarium

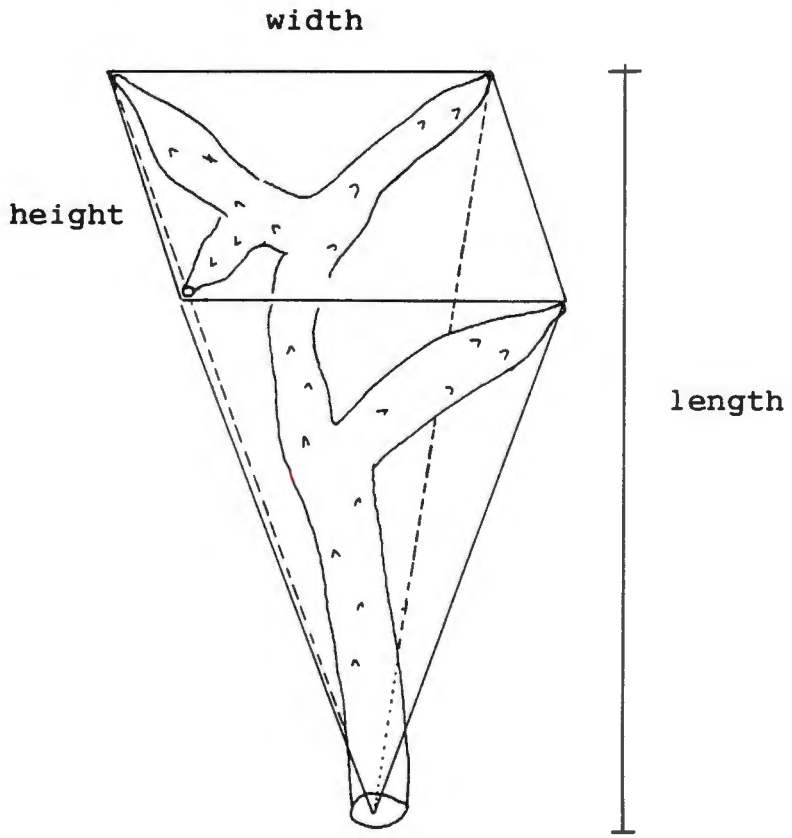


Fig. 1: The morphometric measurements taken from A. austera fragments. The volume enclosed proved to be approximately that of a pyramid, the basal area of which was given by the fragments greatest width and height. This index of volume was considered to be the best denominator for the rather abstract term "size". The area of contact between the fragment and the substratum was calculated as the triangle determined by greatest width and length.

the fragments were maintained in flow through sea water tanks at light levels roughly comparable to those on the reef (unpubl. data). Light levels were recorded with a LI-COR Model 185 quantum photometer/radiometer.

As colony size and shape obviously must have an influence on the formation and the shape and size of fragments, the morphometrics of whole colonies were measured in the vicinity of the sample sites. Parameters measured were colony length, width, height. From these measurements colony volume was calculated, considering the space occupied by the colonies as a rectangle; also average branch length, average branch width was measured and the number of unattached fragments situated within 50cm radius of each colony were counted.

Data were analysed using standard statistical techniques (Zar, 1984). Differences in morphometrical measurements between the size classes were tested by means of factorial multiway Analysis of variance using general linear model procedure due to unequal replication. Subsequent comparisons of groups were done by means of Tukey's test. Due to survival categories being on an ordinal scale all correlations of morphometrical variables on survival classes are rank correlations using Kendall's coefficient. Where applicable, simple linear and multiple linear correlations were used.

Results

1) depth, colony size and amount of fragment

The influence of colony size and shape on the production of fragments was investigated at different depths.

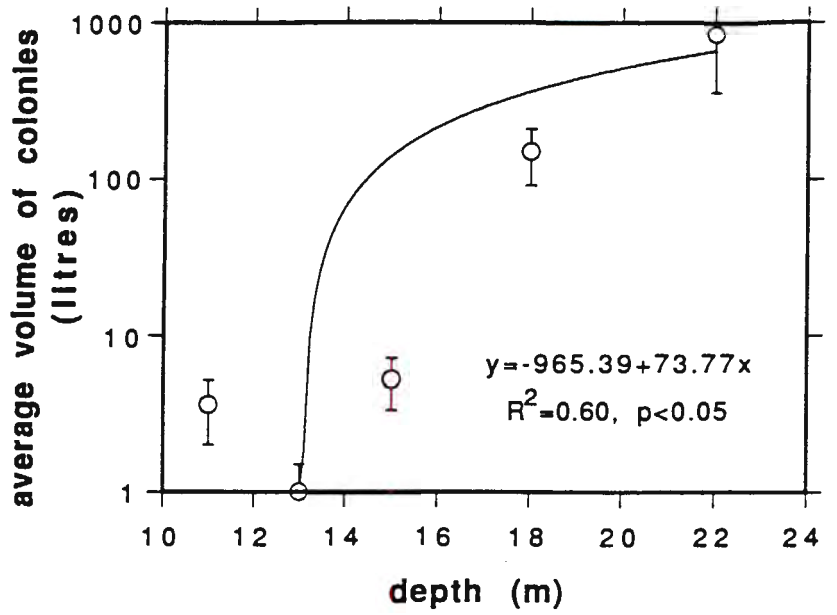


Fig. 2: Relationship between colony volume and depth. The logarithmic scale on the y-axis causes the linear regression line to bend. The formula is for a linear regression.

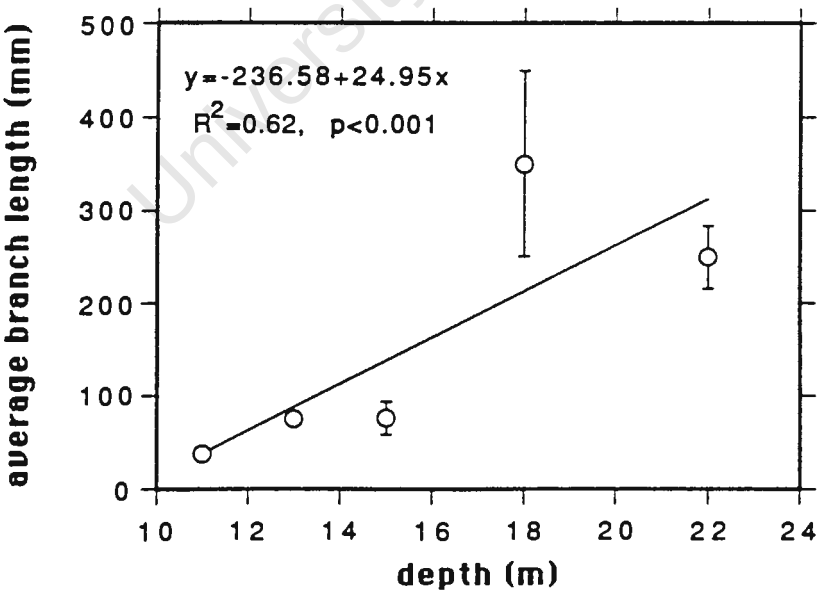


Fig. 3: Relationship between average branch length on unbroken colonies and depth.

Multiple regression analysis showed a significant relationship between depth and colony length, width, heigth, volume, average branch length and average branch diameter (ANOVA for full regression: $F=7.39$; df: 6, 16; $R^2=0.73$, $p<0.001$; Durbin-Watson statistic: 1.114).

The volume of the colonies was significantly graeter in depths greater than 15m than in less than 15m (t-test, $t=-2.12$, $p<0.05$), and there was a positive correllation between depth and colony volume ($R^2=0.60$, $p<0.05$; Fig.2).

Average branch length and maximal branch width also increased linarly with depth ($R^2=0.62$, $p<0.001$; $R^2=0.79$, $p<0.001$; Figs. 3 & 4). Significant differences existed in the above mentioned parameters between the colonies measured at the different depths (ANOVA, $F=22,1$; df: 2, 20; $p<0.001$; $F=20.6$, df: 2, 20; $p<0.001$ for length and width respectively).

The number of loose fragments encountered within 50cm of the colonies also differed significantly between the depths (ANOVA: $F=6.323$; df: 2,20; $p<0.05$) increasing significantly with depth ($R^2=0.84$, $p<0.05$; Fig. 5).

2) The survival of fragments

Fragment recovery rates depended on the depth of the experimental station. After one month no fragments were recovered at the 12m stations , 52.5% were recovered from the 18m station, and 82.2% from the three pooled 21m stations. Overall recovery was clearly depth-dependent (Fig. 6).

Most fragments did not remain in the same locality, where they were initially deposited but were moved by water motion.

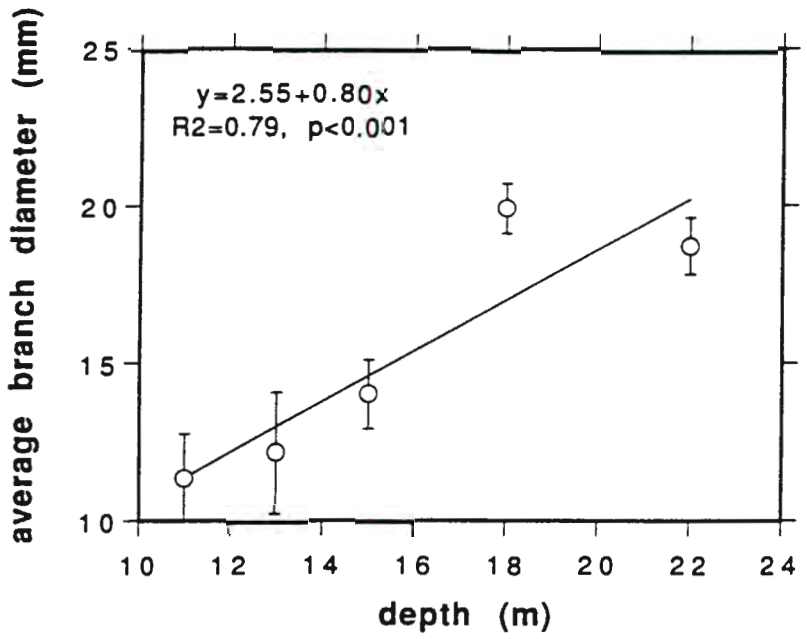


Fig. 4: Relationship between average maximum branch diameter on unbroken colonies and depth.

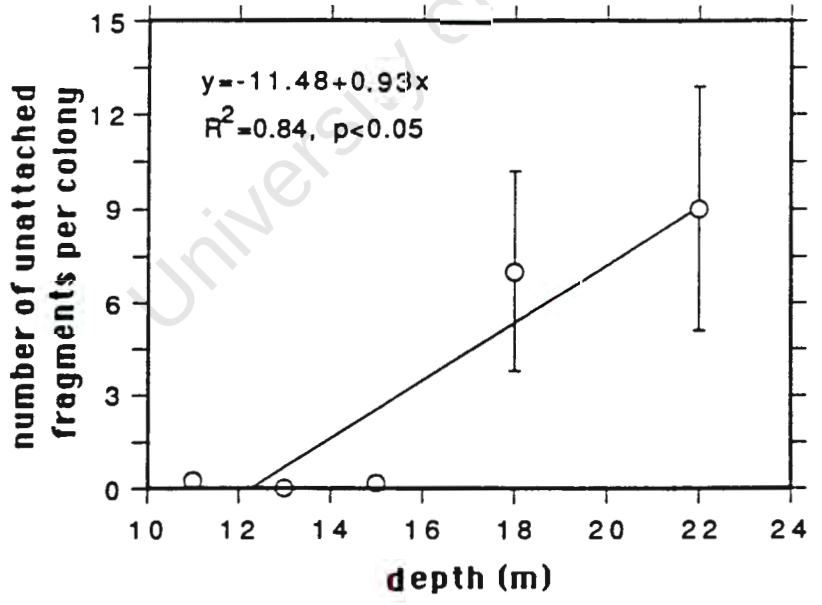


Fig. 5: Relationship between the number of unattached branches found within 50cm radius of colonies, and depth.

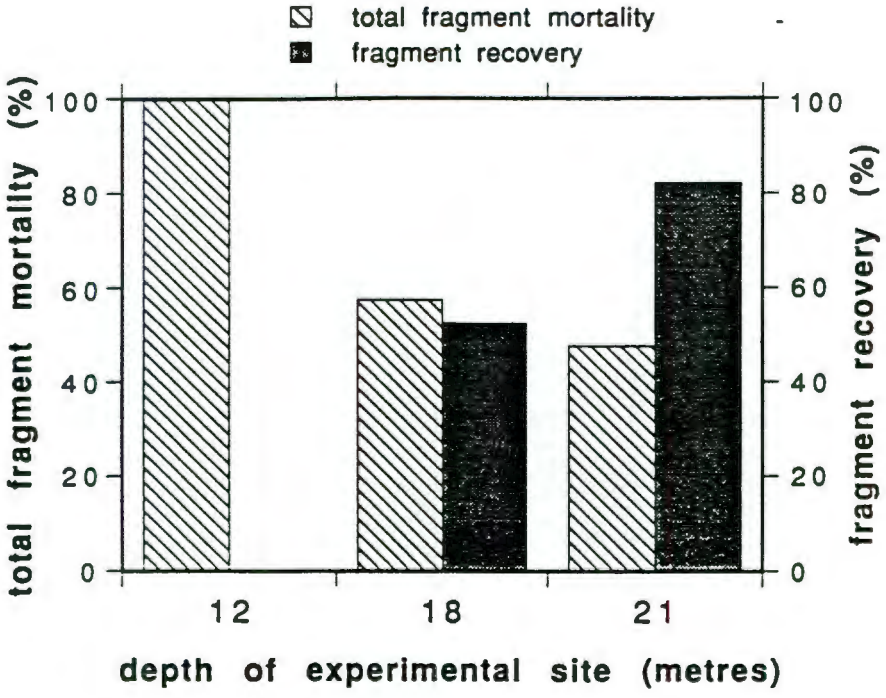


Fig. 6: The relationship between depth, fragment recovery and total (100%) tissue loss on fragments in the first month after breakage from the mother colony.

The slope of the substratum was not important in dispersing fragments. The greatest sloping of the substratum (around 20%) was encountered at the 18m station. High coral cover, however, provided enough obstacles to prevent the fragments from being transported very far and 75% of fragments were recovered within 50cm of the mother colony. At the 21m station, recovery rate within 50 cm was lowest on site 3 (17%) which was situated on sand with no surface structures. The other two sites were situated among prolific coral growth. Site 1 was situated within a shallow depression on the reef, which did not allow fragments to be transported very far and thus led to the highest recovery rate (90%). Site 2 was situated close to a ledge, along which many fragments were transported and recovery rate was lower (30%). Recovery rate therefore depended most strongly on the structural complexity of the substratum, being lowest on the featureless sand plain and highest within the highly structured coral community. On the 12m stations however, all fragments were lost, even though both sub-stations were located amongst equally dense coral growth as at the 18m and 21m stations. One sub-station was situated in a gully, which should have provided at least some shelter from wave action, but still all fragments were lost.

Also survival rates varied with depth (Fig. 6). At the 21m stations 55.6% of all recovered fragments lost up to 50% of their living tissues within the first month, 30% lost all of their living tissues. If those fragments that were not recovered were counted as dead, the total proportion with complete tissue loss would have amounted to 47.7%. At the 18m station 40.9% of recovered fragments lost up to 50% of their living tissue, while 18.2% were recovered completely dead. Again, if lost specimens

were counted as dead, the figure would have risen to 57.5% within the first month. At the 12m stations total recovery failure and therefore assumed total tissue loss accounted for 100% of the fragments.

Testing for differences in shape and size characteristics of fragments in different survival categories was done by comparing the morphometric measurements length, width, height, number of tips, contact area and volume between the survival classes by means of a nonparametric multiway factorial ANOVA using general linear models procedure for unweighed data (Zar, 1984). The results are given in Table 1. After the first month significant differences ($p<0.05$) existed between the survival classes in width, number of tips and contact area (Fig. 7 a-f). Length was almost significant (Table 1) and although differences in volume were very clear, no statistical difference was found due to the large standard deviation (Table 1, Fig 7f). However, rank correlation analysis using Kendall's tau showed all morphometric variables to be correlated with survival (Table 2).

The analysis for survival after the first month showed that two groups existed. One group consisting of all fragments with more than 50% surviving tissues, which had more tips, a greater area of contact and a greater volume than those specimens with less than 50% surviving tissue (Fig. 7 a-f).
Mortality was highest among small, cylindrical fragments (length up to 5cm, width 1cm, consisting of only one single branch tip). Only 13.3% of the original number were recaptured, only 6.6% were

	df after 1 month	F-value after 1 month	significance after 1 month	df after 2 months	F-value after 2 months	significance after 2 months	df after 3 months	F-value after 3 months	significance after 3 months
length	4, 68	2.35	0.0629	3, 14	0.58	0.6360	3, 14	0.32	0.8119
width	4, 68	4.88	0.0016	3, 14	0.98	0.4291	3, 14	0.34	0.7951
height	4, 68	2.32	0.0653	3, 14	3.01	0.0659	3, 14	0.69	0.5710
number of tips	4, 68	4.13	0.0047	3, 14	2.03	0.1554	3, 14	1.19	0.3480
contact area	4, 68	3.42	0.0131	3, 14	0.72	0.5544	3, 14	0.23	0.8734
volume	4, 68	1.57	0.1913	3, 14	0.73	0.5500	3, 14	0.17	0.9132

Table 1: Significance statistics for differences in morphometrics between the survival classes during each monthly stage of the experiment as calculated by multiway factorial ANOVA.

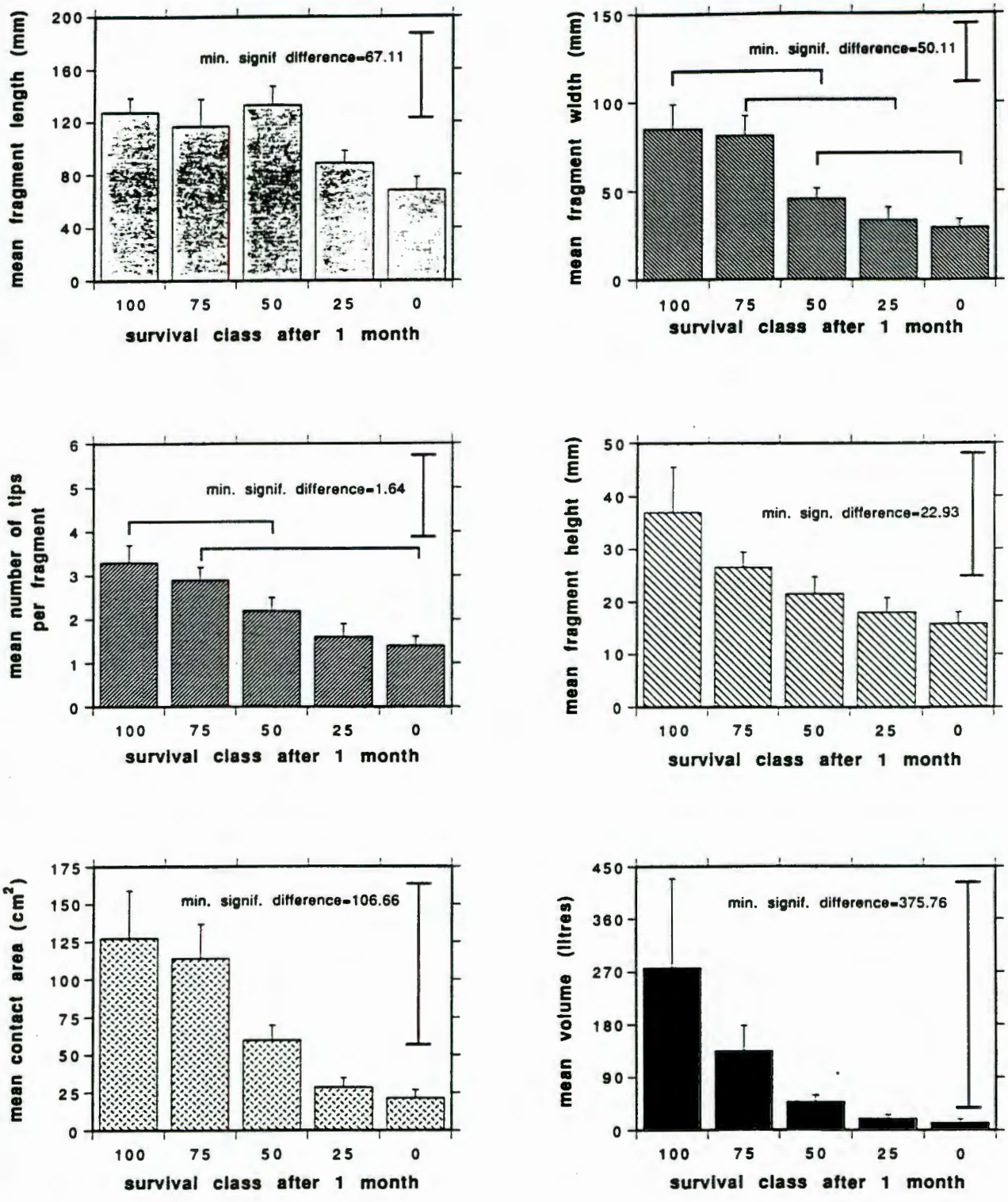


Fig. 7 a-f: Differences in morphometric measurements between the survival classes after the first month. Mean values and significant difference were calculated by multiway factorial ANOVA and used for the significance statistics given in Table 1. Horizontal bars indicate homogeneous groups. Error bars indicate the standard error of the mean.

Rank correlations between morphometrics and survival class

	Kendall's coefficient after 1 month	significance after 1 month	Kendall's coefficient after 2 months	significance after 2 months	Kendall's coefficient after 3 months	significance after 3 months
length	0.2170	0.0140	(0.0153)	0.9362	0.1170	0.5584
width	0.4420	0.0002	0.1209	0.5229	0.1062	0.5825
height	0.2904	0.0015	0.2562	0.1843	0.1290	0.5241
number of tips	0.4360	0.0002	0.3664	0.0662	0.2387	0.2534
contact area	0.4050	0.0006	0.1952	0.2998	0.1623	0.4372
volume	0.4340	0.0002	0.5405	0.0041	0.1051	0.5933

Table 2 : Correlations between morphometrics and survival class during each monthly stage of the experiment.

still alive after one month. This amounts to a possible mortality of 93.4% within the first month for this particular size class.

40 specimens were recovered and transported to the laboratory. There they were given a two week acclimatization period, during which 50% died and were discarded. The remaining specimens were used to continue the survival experiment. This continuation of the experiment only tested the survival of tissues as determined by positioning of the fragments on the substratum, as all fragments were subjected to uniform environmental conditions and wave action could no longer act on the fragments.

After one month in the laboratory, two months after breakage, all fragments were again analysed by means of multiway factorial ANOVA and no differences in either of the morphometric measurement between the survival classes were found (Table 1, Fig. 8, a-f). This indicated that mortality of certain shape groups was due to the influence of physical factors and also that only fragments of a limited morphological range were surviving the second month, due to the loss of specimens with unsuitable sizes and shapes during the field-experiment. To verify this assumption, the measurements of length, width, number of tips, area and volume of the survivors after 2 month were compared to the same measurements from the two distinct groups of survivors after the first month, i.e. the bigger specimens with more than 50% surviving tissues and the smaller specimens with less than 50% surviving tissues. There were no differences in these measurements between the survivors after 2 months and those of the greater 50% survivors after one month, but significant differences in most measurements between the survivors

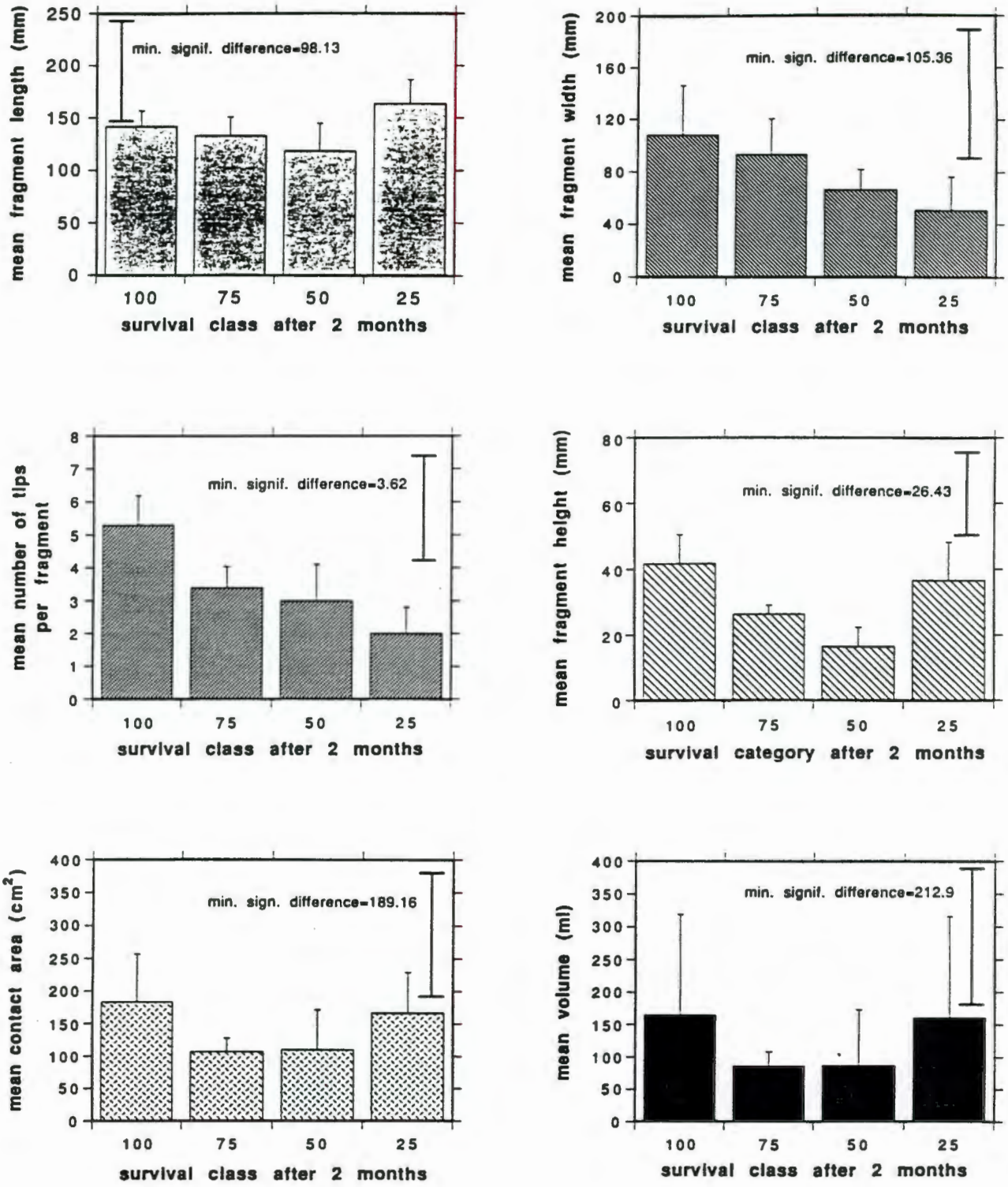


Fig. 8 a-f: Differences in morphometric measurements between the survival classes after the second month. Means and significant difference were calculated by multiway factorial ANOVA and used for the significance statistics in Table 1. The 0% survival class is missing, as it had not been used in this analysis (see text). Error bars indicate the standard error of the mean.

after the second month and the less than 50% survivors after one month (Table 3). The specimens surviving the second month fell within a narrow size and shape range, which seemed to determine their survival during the first month. They were the bigger fragments with more tips and a greater width. This was a consequence of the high mortality of small cylindrical fragments particularly during the first month.

Total mortality during the second month was 63.9%; total mortality in two months after the beginning of the experiment was 75%.

Only 5 specimens survived until the end of the experiment. Total mortality in three months after the date of breakage was 90%. An analysis for differences in morphometrical measurements between the survival classes after the third month showed that no differences existed (Table 1, Fig. 8 a-f).

Other results obtained during the experiment were as follows:
Positioning of the fragments proved to be of importance to tissue survival. The part of the tissue which was in contact with the substratum became necrotic in most specimens. In fragments resting flat on the substratum, the whole underside died off.
The fracture area became overgrown by tissue in 25% of all cases. In the other fragments tissue necroses started to spread from the area adjacent to where the fracture had occurred (75% of all cases).

The analyses showed that the most important factors for fragment survival were the number of tips on the fragment and the maximum

	t-value Group 1 & 2	significance Group 1 & 2	t-value Group 1 & 3	significance Group 1 & 3
length	0.0095	>0.05	5.05	<0.001
width	0.0051	>0.05	3.48	<0.01
height	1.2400	>0.05	(1.59)	>0.05
tips	2.0500	<0.05	3.94	<0.001
area	0.0047	>0.05	3.54	<0.01
volume	0.0007	>0.05	2.88	<0.01

Table 3: Differences in morphometrics between surviving fragments after the first and second month. Group 1 are all fragments after the second month, Group 2 are the fragments with more than 50% surviving tissues after one month, Group are the fragments with less than 50% surviving tissues after one month. The result shows that Groups 1 and 2 only differ in number of tips.

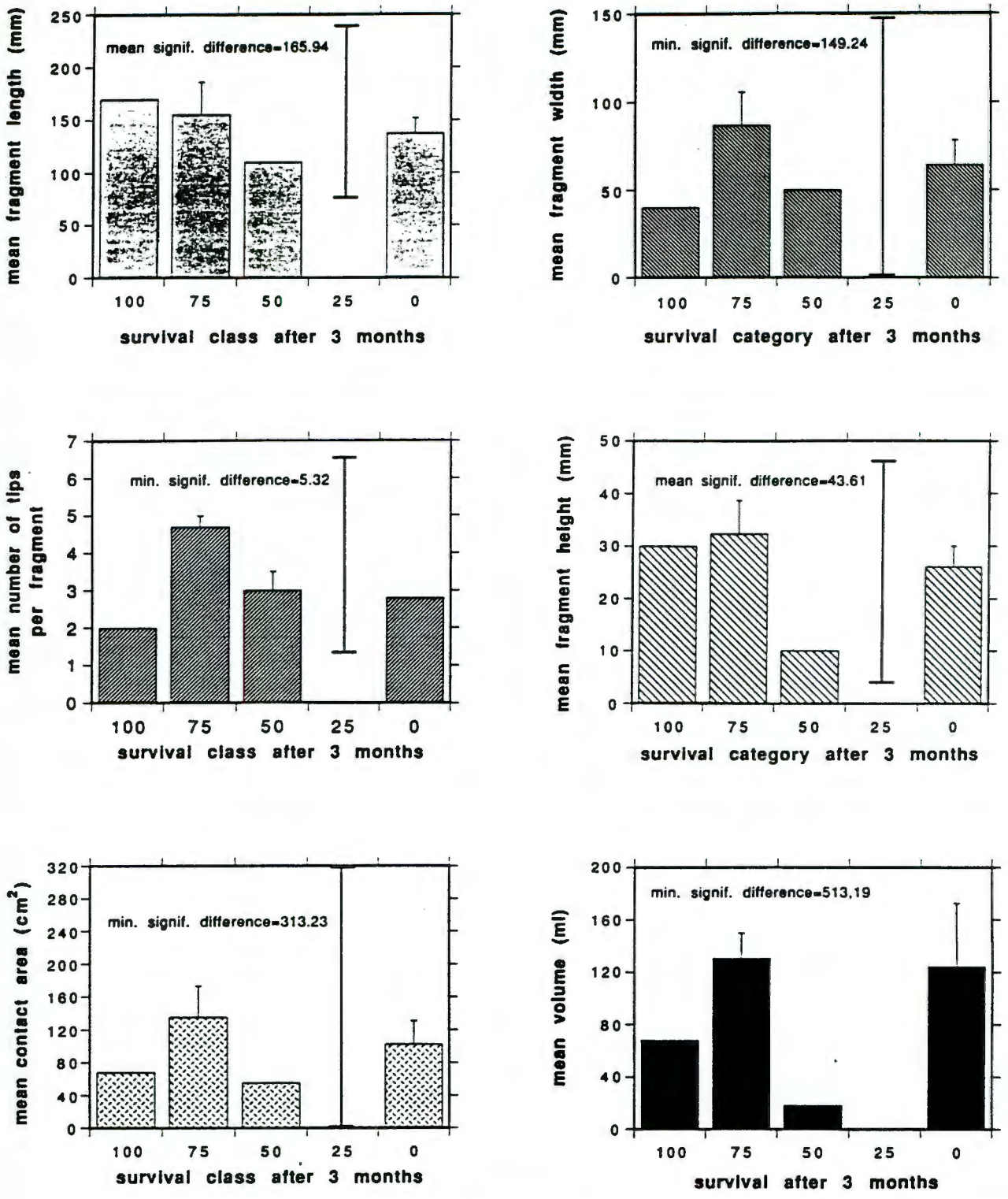


Fig. 9 a-f: Differences in morphometric measurements between the survival classes after the third month. Means and significant difference were calculated by multiway factorial ANOVA and used for the significance statistics in Table 1. No 25% survivors were recorded after three months. Columns without error bar indicate a single specimen in the survival group. Error bars indicate the standard error of the mean.

width of the fragment; of lesser importance were the indices of contact area and volume.

c) skeletal regeneration

For obvious reasons, skeletal regeneration is linked to tissue regeneration over the broken area and was only observed in 17.7% of all fragments. The first step of skeletal regeneration was coverage of the broken area with a continuous, new coenosteum after a continuous layer of tissue had become established. Following this, the axial corallite would often regain its position as the growing tip and start depositing calcium, leading to an extension of the skeleton in the opposite direction of the previous growth direction (50% of cases, Figs. 10 & 11). After a month, however, no highly organised, growing branch tip had yet been formed. Newly forming radials, which were present in 13 out of 16 specimens showing skeletal regeneration of the fracture area, did not group around the axial in a typical manner. In some specimens the first radials of the first rosette were just differentiating.

From randomly collected fragments it became obvious that with time a second complete branch tip was formed.

The observed corallite growth on the broken areas was 1.25mm (S.D.=0.25, range 0.5-2.4mm) with an average of 3 (S.D.=2.8, range 0-8) corallites formed in one month.

Discussion

Species of the genus Acropora are typical of the tropical Indo-Pacific, decreasing in abundance and species richness towards the limits of the reef belt (Veron & Wallace, 1984). This situation is

Fig. 10: A regenerated fracture area. The presence of spiny coenosteum proves that the entire area was covered by living tissue. A new axial corallite with attending radial corallites was formed (magnification x5).

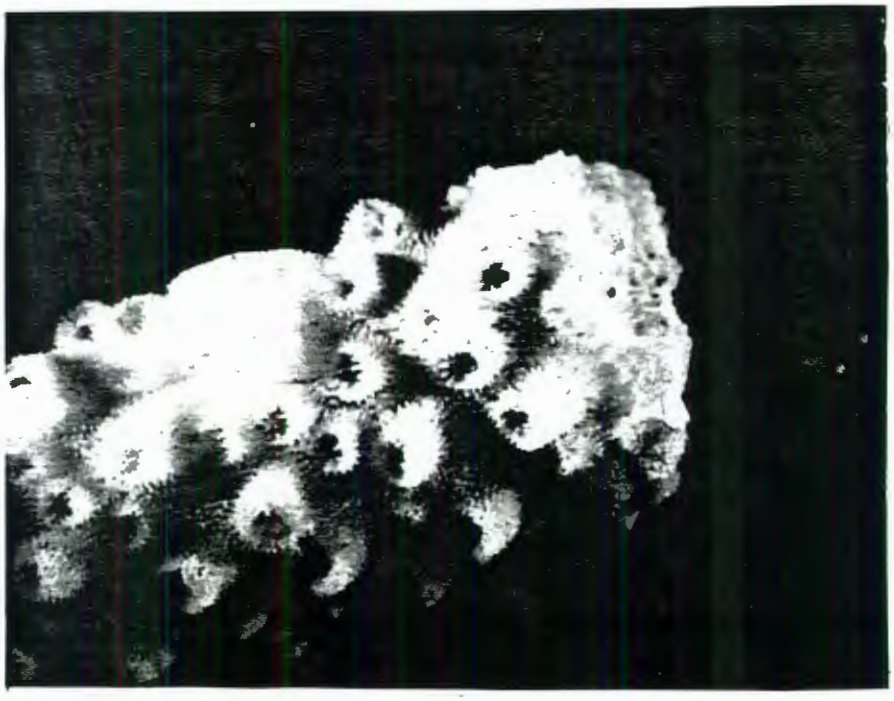


Fig. 11: A fracture area without any signs of regeneration. No new coenosteum was deposited over the fracture area, indicating that it was not covered by living tissue (magnification x5)

also true for South Africa. There are numerous indications in the results of the present study suggesting, that conditions on South African reefs are marginal for fragmenting Acropora. The observed high mortality of fragments casts doubt on the success of asexual reproduction under the harsh local conditions. The distribution and different morphologies of the colonies on the reefs is also of importance. Colonies in the shallow water, which are subjected to much stronger wave action, were much smaller, had much shorter branches and showed no sign of asexual reproduction by fragmentation. Although branches were thinner on the shallow reef, the shorter branches might be less likely to brake as they experience less drag (Vogel, 1981). The experiment showed clearly that chances for fragment survival in shallow depths were slim. Although the fragments used in the shallow sites were placed in relatively sheltered areas of comparable structural complexity to the deep sites (one site in aflat area with rich coral growth and one site inside a gully), none of the experimental fragments survived. As wave action decreases with increasing depth (Denny, 1988), this result indicates, that water movement by wave action can directly act on fragment survival, by means of displacing them and depositing them in unfavourable habitats, such as the sandplains surrounding the reefs, or by damaging them beyond their ability to regenerate. This mechanism appeared to lead to the death of all fragments in the shallow sites. The only reef-zone where fragments seemed to have reasonable survival chances was situated below 18m depth. There, A. austera was a dominant member of the community. It appeared that fragmentation was a common way of reproduction on 4-Mile Reef, as numerous reattached fragments

were observed, and some colonies seemed to consist mainly of reattached fragments.

It was also very clearly shown that survival, particularly in the first month in field conditions, was linked primarily to the shape of the fragments, as characterized in this study by length, width, height and number of tips. Number of tips and width were the only measurements which differed significantly between the survival categories in the field experiment (Fig. 7). It appeared, that the ideal shape of the fragments constituted of the following traits: a great width, i.e. at least two widely spreading branches which give stability against lateral displacement and rolling over, and numerous tips, which assure that parts of the fragment cannot be smothered if resting on a sandy substratum, or damaged by rolling around. In support of this hypothesis is the fact that mortality was always highest in small, cylindrical fragments but much less in equally small fragments with a large number of tips or widely spreading branches. This fact is reflected by the absence of any significant differences between the survival categories in length or height, but only in width and number of tips (Table 1, Fig. 7). Therefore I suggest that it is neccessary to add to the postulated "size-dependent survivorship hypothesis" (Loya, 1976; Highsmith et al., 1980; Hughes, 1989; Lewis, 1991) at least in this particular case, a "shape-dependent survivorship hypothesis".

A second particularly important factor in fragment survival was the way in which fragments came to rest on the substratum. As the tissues in direct contact with the substratum showed a clear tendency for necrosis, it was obvious that cylindrical fragments, or those with low three dimensionality, were at a disadvantage. The more branches there were on the fragment and the more

"contorted" its shape, the higher was the amount of tissue lifted off the substratum and likely to survive.

It is interesting to note that in the deep sites there was no relationship between the type of inanimate substratum on which the fragments were placed and their survival rate. One may have expected a higher mortality on sand than on rock, due to smothering by sediment. However, because of the high mobility of the fragments, most were transported away from the flat sandy areas and deposited in a much more favourable substratum, as they often got caught between other corals or against rocky ledges. This high mobility of the fragments however lead to the loss of all experimental specimens in the shallow sites.

All observations in the present chapter hold true only for fragments which did not come to rest on the mother colony. In this case, fragment shape did not seem to play a role and reattachment appeared to be fast. Most colonies actually gave the appearance of a chaotic mass of broken and reattached branches. Due to the open arborescent growth form most branches probably get caught on a neighbouring branch and come to rest on the same colony. It is unclear how many fragments are actually exported from the mother colony. It is possible that mechanisms similar to those decribed by Chornesky (1991) for the Caribbean Agaricia tenuifolia also act on A. austera. In Agaricia tenuifolia intraspecific contact lead to fusion of fragments and colonies leading to increased stability (Chornesky, 1991).

The regrowth of tissues over exposed fracture areas should, according to literature, be the first step to recovery and reattachment in broken corals (Loya, 1976; Bak et al., 1977; Rogers et al., 1982; Rinkevich & Loya, 1989). This situation was,

however, recorded only in a minority of cases in the present study. From randomly collected fragments and field observations it became apparent that lesions at the growing tip were much more often covered than lesions at the base of the coralla. While numerous fragments with completely dead bases were observed, no such situation was ever found at a corallum's tip, even if it had been broken previously. This situation can probably be explained by the coral's natural growth pattern (Chadwick & Loya, 1990), with most energy being translocated towards the tip (Barnes & Chalker, 1990). When regeneration of the broken base took place, the Acropora austera fragments developed a second growing tip, which, with time, took on the same morphology as the original one, thus ensuring extension of the now unattached fragment in two directions. Reattachment never seemed to be initiated by the basal parts of the fragment which was either given up, or regenerated as a second growing tip. Reattachment was most often observed to take place by means of a hard tissue proliferation arond a suitable object, roughly comparable to the "filling response" described by Lang & Chornesky (1990) for competitive encounters. In most cases of successful reattachment these were other branches of the same mother colony. Reattachment to bare ground was rarely observed. Allografts between A. clathrata and an A. austera fragment were observed in two cases.

Conclusion

The results in this chapter indicate, that wave action is a major forcing factor of South African coral communities. This has been achieved via the evaluation of coral colony shapes and fragment survival in different wave exposure and fragment survival.

Acropora austera colonies in shallow water were much smaller and had shorter branches than colonies in deep areas. There was no indication that fragmentation can be a viable mode of reproduction in shallow, wave-swept areas, in contrast to the situation in deep, more protected areas. It has also been demonstrated that in a South African Acropora austera population the survival of fragments not only depended on size, but more importantly on shape, the most important parameter being the number of tips on the fragment. I therefore suggest a "shape-dependent survivorship" hypothesis, which is possibly applicable to a wide variety of fragmenting coral species.

Literature cited:

Bak, R.P.M., J.J.W.M. Brouns & F.M.L. Heys. 1977. Regeneration and aspects of spatial competition in the scleractinian coral Agaricia agarites and Montastrea annularis. Proc. Third. Int. Coral Reef Symp., University of Florida, Miami: 143-148.

Barnes, D.J. & B.E. Chalker. 1990. Calcification and photosynthesis in reef-building corals and algae. in: Dubinsky, Z. (ed.): Coral Reefs - Ecosystems of the world 25; Elsevier Amsterdam-New York: 109-131.

Chadwick, N.E. & Y. Loya. 1991. Regeneration after experimental breakage in the solitary reef coral Fungia granulosa Klunzinger, 1879. J.Exp.Mar.Biol.Ecol. 142: 221-234.

Chornesky, E.A. 1991 The ties that bind: inter-clonal cooperation may help a fragile coral dominate shallow high energy reefs. Mar.Biol. 109: 41-51.

DeVantier L.M. & R. Endean. 1989. Observations of colony fission following ledge formation in massive reef corals of the genus Porites. Mar.Ecol.Progr.Ser. 58: 191-195.

Denny, M. 1988. Biology and the mechanics of the wave-swept environment. Princeton University Press.

Highsmith, R.C. 1982. Reproduction by fragmentation in corals. Mar.Ecol.Progr.Ser. 7:207-226.

Highsmith, R.C., A.C. Riggs & C.M. D'Antonio. 1980. Survival of hurricane generated coral fragments and a disturbance model of reef-calcification/growth rates. Oecologia 46: 322-329.

Hughes R.N. 1989. A functional biology of clonal animals. Chapman & Hall, London.

Lang, J.C. & E.A. Chornesky. 1990. Competition between scleractinian reef corals-a review of mechanisms and effects. in: Dubinsky, Z. (ed.): Coral Reefs - Ecosystems of the world 25; Elsevier, Amsterdam-New York: 209-252.

Lewis, J.B. 1991. Testing the coral fragment size-dependent survivorship hypothesis for the calcareous hydrozoan Millepora complanata. Mar.Ecol.Progr.Ser. 70: 101-104.

Loya, Y. 1976. Skeletal regeneration in a Red Sea scleractinian coral population. Nature, London 261: 490-491

Mah, A.J. & C.W. Stearns. 1986. The effect of Hurricane Allan on the Bellairs fringing reef, Barbados. Coral Reefs 4: 169-176.

Riegl, B. & B. Velimirov. 1991. How many damaged corals in Red Sea reef systems? A quantitative survey. Hydrobiologia 216/217: 249-256.

Rinkevich, B. & Y. Loya. 1989. Reproduction in regenerating colonies of the coral Stylophora pistillata. in: Spanier,

E. et al. (eds.): Environmental quality and ecosystem stability: Vol IV-B, Hebrew University, Jerusalem, Israel, pp. 257-265.

Rogers, C.S., T.H. Suchanek & F.A. Pecora. 1982. Effects of hurricanes David and Frederic (1979) on shallow Acropora palmata reef communities: St. Croix, U.S. Virgin Islands. Bull. Mar. Sci., Vol.32, pp. 532-548.

Tunnicliffe, V. 1981. Breakage and propagation of the stony coral Acropora cervicornis. Proc. natn. Acad. Sci. USA. 78: 2427-2431.

Veron, J.E.N. & C.C. Wallace. 1984. Scleractinia of Eastern Australia. Part V. Family Acroporidae. Aust.Inst.Mar.Sci. Monogr.Ser., Australian National University Press, Canberra.

Vogel, S. 1981. Life in moving fluids. Princeton University Press.

Wallace, C.C. 1985. Reproduction, recruitment and fragmentation in nine sympatric species of the coral genus Acropora. Mar. Biol. 88: 217-233.

Yap, H.T, P.M. Alino & E.D. Gomez. 1992. Trends in growth and mortality of three coral species (Anthozoa:Scleractinia), including effects of transplantation. Mar.Ecol.Progr.Ser. 83: 91-101.

Zar, J.A. 1984. Biostatistical analysis. Second edition, Prentice-Hall, New Jersey.

MODELLING THE EFFECTS OF SEDIMENTATION ON THE ENERGY BUDGETS OF FOUR HARD AND FIVE SOFT CORAL SPECIES

Abstract

The physiological reactions of four hard coral species (Favia favus, Favites pentagona, Platygyra daedalea, Gyrosmilia interrupta) and five soft coral species (Lobophytum depressum, Lobophytum venustum, Sinularia dura, Sinularia leptoclados, Sarcophyton glaucum) from South Africa to sedimentation were observed in the laboratory. Natural sedimentation levels and light conditions were simulated, and carbon production and respiration of all species were measured by respirometry; carbon output through mucus production was measured directly. The results were used to model daily energy budgets for these species, assuming two models, one allowing for 50% PARs (photosynthetically active surface irradiation) and one for 25% PARs. The models showed severe productivity losses as well as decreased respiration under sedimented conditions. P/R ratios of all species, which were above 1 in the absence of sediment, dropped below unity when the corals were subjected to sedimentation. While overall respiration dropped, its share in photosynthetically produced carbon rose dramatically. In control conditions mucus output amounted to 35% of daily respiration, while in sedimented conditions this figure rose to 65%. Sedimentation therefore acts on coral metabolism by decreasing photosynthetic production, increasing relative respiration and increasing C-loss through greater mucus output.

Introduction

Numerous studies have described the behavioural and growth reactions of hard corals to sedimentation (Bak & Elgershuizen, 1976; Lasker, 1980; Rogers, 1983; Laboute, 1988; Rice & Hunter, 1992; Stafford-Smith & Ormond, 1992; Stafford-Smith, 1993), but relatively few studies exist on their physiological responses. Reports in literature indicate severe interference of sedimentation with coral energetics (Szmant-Froehlich et al., 1981; Dallmeyer et al., 1982; Abdel-Salam & Porter, 1988), but further information about the exact mechanism of interference needs to be elucidated. Sedimentation could act on the corals by reducing available light and, therefore, photosynthetic production, and/or by increasing respiration either due to increased activity of the polyps (Bak & Elgershuizen, 1976; Stafford-Smith, 1993) or due to increased mucus output. Mucus, and the formation of mucus sheets, are an integral part of the coral's response to the environment, particularly to sedimentation (Coffroth, 1988). The importance of mucus for coral energetics has long been recognized (Benson & Muscatine, 1974; Richman et al., 1975) and anecdotal observations on increased mucus production due to sedimentation are plentiful (Bak & Elgershuizen, 1976; Rogers, 1990; Stafford-Smith & Ormond, 1992; Stafford-Smith, 1993). However, a quantification of possible changes in mucus output has not yet been attempted. The present study attempts to quantify the importance of each component of the effects of sedimentation seperately. Using a modelling approach the effects of the coral's reactions are then integrated and the influence of sedimentation on the daily energy budgets of the corals are derived.

Most physiological studies have been performed on Atlantic coral species (Szmant-Froehlich et al., 1981; Dallmeyer et al., 1982; Peters & Pilson, 1985; Abdel-Salam & Porter, 1988), while little information is so far available on the responses of Indo-Pacific hard coral species (Yamasu & Mizofushi, 1989). Soft corals have so far been completely ignored and only speculations and indirect evidence concerning their tolerance to sedimentation can be found in the literature (Dinesen, 1983; Dai, 1991). In many coral reefs, especially in South Africa (see Part II), they form a significant percentage of the total coral cover. As sedimentation is believed to be a forcing factor underlying community patterns in South Africa (Part II) and elsewhere (Dinesen, 1983; Done, 1983; Dai, 1991), the processes underlying these patterns cannot be understood unless the major components of the community have been investigated.

In order to assess the importance of sedimentation on a coral community, information is needed about its effects on coral energetics and possible differences in the reaction of different taxa. In the present study I have made an effort to chose species which were dominant in particular environments (see Part II) in order to be able to relate the physiological results to observed community patterns on the reefs.

The aims of this study were: 1) to assess differences in production and respiration under sedimented and unsedimented conditions in selected hard and soft coral species; 2) to model the importance of sedimentation under different light regimes which correspond to different depths; 3) to test whether differences exist in mucus production under sedimented and unsedimented conditions; 4) to quantify the carbon loss due to

mucus production and export; 5) to identify which component of the effects of sedimentation creates the stress, and 6) to see whether differences exist in the physiological reactions of the tested species.

Materials and methods

The work was conducted on corals collected from the Maputaland reef systems in northern Natal, South Africa. Nine species of coral were studied: four hard coral species (Favia favus, Favites pentagona, Platygyra daedalea, Gyrosmilia interrupta) and five soft coral species (Lobophytum patulum, Lobophytum depressum, Sinularia dura, Sinularia leptoclados and Sarcophyton glaucum). These species were chosen for their differences in growth form and differences in their typical habitats on the reefs (see Part II). As in situ measurements were impossible due to the off-shore locality of the reefs (see Part II), six colonies of each species were collected and brought back to the laboratory in Durban. The animals were maintained in flow-through tanks containing filtered sea-water at a constant, thermostat-regulated temperature of 21°C. Light levels were similar to natural conditions on the reefs (unpubl. data). Light intensities were measured with a LI-COR Model 185 quantum photometer/radiometer. Corals were allowed to adapt to laboratory conditions for 6 weeks prior to the experiments.

Respiration and photosynthesis

Oxygen production and respiration were measured using a 7-chambered respirometer. Each chamber was fitted with a stirring pedal, driven by an electrical motor, and a YSA model 57 Oxygen probe allowing simultaneous readings of dissolved oxygen levels in

all 7 chambers. The oxygen probes were standardized using Winkler-titrations (Strickland & Parson, 1972) prior to and at the end of each test series. The chambers were maintained at a constant temperature of 21°C, comparable to the average winter water temperature within the Agulhas current, within which the reefs are situated (Schumann, 1988; Beckley & van Ballegooyen, 1992). The experiment was conducted in mid-winter (July/August, southern winter) with animals collected during the same season.

Respiration and production were measured on the same animals under identical light regimes both with and without applied sediment. Each data point represents the mean of measurements taken on 4-6 animals in 5 runs. During the trials water samples were drawn from the chambers and controlled for changes in phosphate and nitrate levels, as indicators for changes in water chemistry (Szmant-Froelich et al., 1981).

In production experiments the baseline from which O_2-increase was measured was set at ambient oxygen saturation, which was between 80 and 85% (6.1ppm). In respiration experiments corals were allowed to respire until oxygen levels had dropped to 50% saturation, as over this range the falling oxygen concentration had no effect on the respiration rate (Spencer-Davies, 1991).

Photosynthesis was measured under five different light levels. Light levels were measured using a LI-COR 185 quantum radiometer/photometer connected to an underwater probe and an above-water probe. The low light levels (10 and 40 $Wm^{-2}s^{-1}$ were provided by a bank of four full spectrum daylight tubes (Astra 40W, B 2.1 Colour match/55), mounted over the respirometer chambers, which was enclosed by white, reflecting surfaces to allow homogenous reflection. The other light intensities (75, 150,

300 $Wm^{-2}s^{-1}$ were obtained by differential shading in daylight, using shade cloth (Titlyanov, 1991).

Immediately after each oxygen production measurement, the respirometry chambers were covered in black plastic and respiration was measured. Thus the measurements of the respiration rate corresponded to the previously observed production rate.

After the experiments all corals were decalcified in a solution of 15% sodium citrate and 50% formic acid in order to obtain exact weights. All weights are expressed as wet tissue weight. For weighing, the decalcified animals were squeezed dry and put for one minute on a water absorbing cloth in order to remove all excess water from the canal system within the animals. Only when no more water could be drawn from the tissues were they weighed.

Sedimentation procedures

Locally-collected sand was burnt in a muffle furnace at 350°C for two hours to eliminate the organic component. A grain size analysis using a settling tube showed it to consist of 0.1% very coarse sand, 0.6% coarse sand, 46.1% medium sand and 53.4% fine sand; medium grain size was 0.253mm. Of the clean sand, a constant quantity of 14.18g, which amounted to a sediment load of 200mgcm^{-2} for the respiration chamber, was applied to the corals. This sedimentation level was chosen because it compared well to the observed sedimentation levels on South African reefs (Part II) and also because it had frequently been used in previous studies (Rogers, 1990; Stafford-Smith, 1993). The sediment was spread as evenly as possible over the bottom of the jars and the corals, which were of different sizes and shapes, covering them with comparable amounts of sand. This ensured that a constant quantity

of sand was confined within the respiration chamber and that the corals were covered with a comparable layer of sand.

Mucus analysis

The colonies used for the respiration experiments were also used for mucus analysis. Before incubation was started, the colony surface was cleaned of organic and inorganic materials by means of a gentle jet of filtered sea water. The specimens were placed at ambient temperature in 500 ml sterilized containers with 0.2 um filtered sea-water for three hours. Oxygen saturation of the water was 83%, determined by Winkler titrations (Strickland & Parson, 1972) and lighting was constant at around $50Wm^{-2}s^{-1}$. For control conditions each specimen was placed in a jar and left for three hours. After removal of the corals from the jars, the water was stirred for 5 minutes to aid mucus precipitation (Herndl & Velimirov, 1985) and then filtered through a preweighed filter (47mm diameter, 0.2um pore size), rinsed with ammonium formate to elute salt residues and stop bacterial activity, then with 0.5N H_2SO_4 to elute free carbon, and finally with 5ml distilled water. The filters were dried at 70°C for 24 hours and weighed.

For conditions with sediment application the specimens were placed in a preweighed, premuffled aluminium dish in sterilized jars, and $200mgcm^{-2}$ sterile sediment were applied. The rest of the procedure was identical to that used under control conditions. After incubation all sediment was collected off the animals by means of a gentle jet of the same water as used during the incubation. The water was decanted and filtered, the trays were dried for 24 hours at 70°C, weighed and afterwards burned at 350°C for 1.5 hours. Carbon content of the mucus was determined by burning the samples

in a helium/oxygen flame in a Perkin-Elmer 2400 CHN Micro Analyser.

All data are based on two experimental runs with five animals per species.

Modelling

It was decided to integrate all measurements of the coral's responses to sedimentation by a modelling approach. As the experiment was conducted in mid-winter, light conditions for a clear, cloudless mid-winter day (southern winter, July) were used for modelling 24h production. Surface light conditiones (PARs, photosynthetically active radiation on the surface) were measured with a LI-COR 185 quantum radiometer/photometer connected to an above-water probe, taking hourly readings over the entire daylight period starting one hour before dawn and ending one hour after dark. The measurements of three days were averaged to provide the light intensities for the model day (Fig. 1). Maximum irradiance levels in Natal are around 600 $Wm^{-2}s^{-1}$ in Winter and over 1000 $Wm^{-2}s^{-1}$ in summer. The light conditions on the reefs were measured during the winter and spring months June, July, August and September at 10m depth, using the same LI-COR 185 radiometer/photometer, this time connected to an underwater probe. Light attenuation at 10m depth was found to vary between 50 and 75%, depending on water clarity. Using these measurements, the experimental procedure and the frame for the modelling exercise employed $300Wm^{-2}$ as maximum irradiance for production measurements. This level corresponds to maximal illumination for winter at a 10m-deep site (50% light attenuation), when the water is usually clear, and an average scenario for summer, when the water is usually murky (75% attenuation). The other light levels

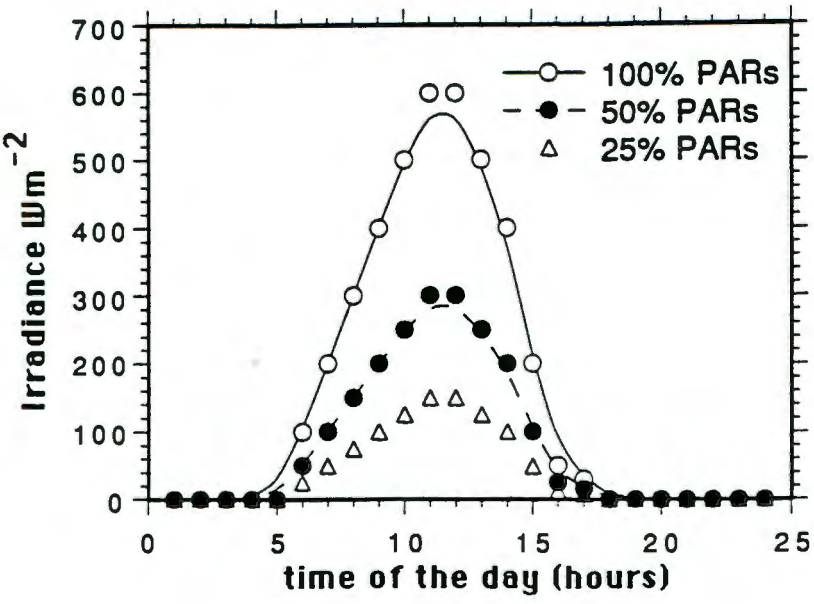


Fig. 1: PAR (photosynthetically active radiation) levels observed on clear winter days in July in northern Natal (solid line, 100% PARs= PAR on the surface) from which irradiance levels for the models were derived (dashed line 50% PARs, dotted line 25% PARs).

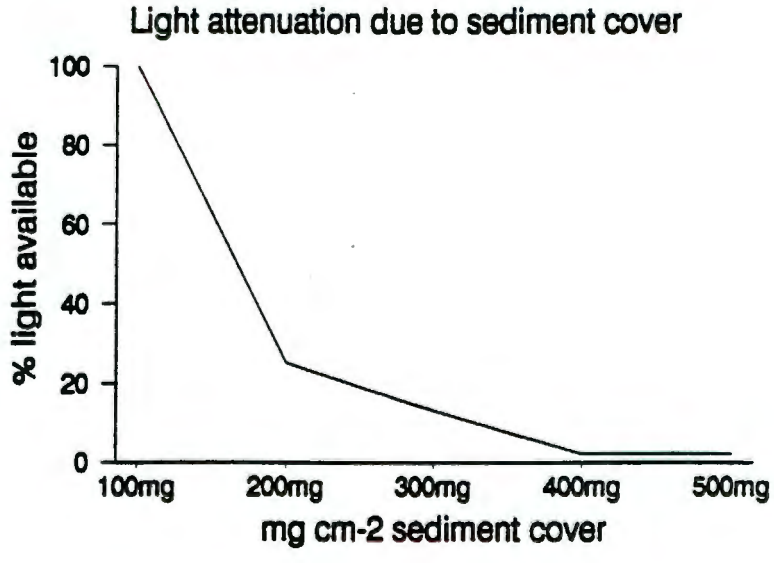


Fig. 2: Light attenuation caused by different levels of sediment application onto a flat plexiglas plate with an attached irradiance meter, simulating a flat coral.

used in the experiment were chosen to provide more or less equally interspersed data points between the extremes (10 $Wm^{-2}s^{-1}$ to 300 $Wm^{-2}s^{-1}$).

The theoretical irradiance curves for the models were calculated from the surface irradiance data for 25% PARs and 50% PARs (Fig. 1). Using these assumptions, energy budgets could be calculated for theoretical sites at approximately 10m (50% PARs) and 15m depth (25% PARs) in clear water conditions, and at 10m in murky conditions (25% PARs). For the calculation of daily production and respiration, the production and respiration data obtained in the laboratory experiments were fitted to the calculated 24h irradiance curves. The area under the bell-shaped curve was integrated to provide an estimate of total production and respiration over a 24h period. From these values average daily P/R ratios were calculated. Mucus production was assumed to be constant over the full 24h period (Crossland et al., 1980) and could therefore also be integrated into the model.

Results

a) The effect of sediment application on available light

The amount of light extinction caused by various loads of sediment was estimated by covering a plexiglass plate, under which a light sensor was attached, with sediment. The results of this simple experiment are given in Fig.2. It showed that on a flat surface even 100mg sediment/cm^{-2} caused a 75% reduction of available light. From 400mgcm^{-2} onwards light attenuation remained constant at around 97% (Fig. 3).

b) Overall production and respiration characteristics

The production and respiration data obtained from the four hard coral species and the five soft coral species were tested against each other in two separate analyses by means of factorial Analysis of Variance (Zar, 1984). The analysis tested for the influence of species, individuals, replicates (with replicates being nested into individuals), light, sedimentation and the interaction between light and sedimentation on the production and respiration values. For the hard corals the results showed that the measurements of individuals and replicates had no influence on either production ($F=0.19$, $df:3$, $p=0.90$ in the absence of sediment; $F=1.01$, $df:12$, $p=0.44$ in the presence of sediment) or respiration ($F=0.58$, $df:3$, $p=0.63$ in the absence of sediment; $F=1.18$, $df:12$, $p=0.29$ in the presence of sediment), which proved homogeneity between individuals and replicates. Significant influence on the production and respiration values was exerted by sand ($F=18.21$, $df:1$, $p=0.001$), light level ($F=23.51$, $df:4$, $p=0.001$) and interaction of sand with light, when both factors were modelled as equally weighed ($F=2.77$, $df:4$, $p=0.027$). This situation is well illustrated by Fig. 3. There were differences between the species in respiration ($F=4.07$, $df:3$, $p=0.0072$), but not in production ($F=2.18$, $df:3$, $p=0.09$). A subsequent Tukey test for studentised range showed that differences in respiration existed between Favites pentagona and Platygyra daedalea, but not between the other species. Significant differences (at the 5% level) were also revealed by this test between production by Favites pentagona and Gyrosmilia interrupta as well as between Platygyra daedalea and Gyrosmilia interrupta. These differences were however not sufficient to influence the general model. A

similar analysis testing for differences in production and respiration between the species in control- and sedimented conditions showed less differences in production in sedimented conditions. In respiration the hard corals formed a homogenous group both with and without sediment (Fig. 7 a & b).

The photosynthesis/irradiance curves of all species suggested that light saturation had not yet been fully achieved at an irradiance level of $300Wm^{-2}s^{-1}$ (Fig. 3). The relative loss in production due to sedimentation was greater at high light levels than at low light levels (Fig. 3).

In all hard corals, except Cyrosmilia interrupta, there existed a linear relationship between respiration and light level (Fig. 4). As production was also positively correlated with light, this raised the possibility that respiration and production are also correlated. This proved to be the case for two of the species (Favia favus and Platygyra daedalea) in the absence of sediment, but none in the presence of sediment (Fig. 5).

The same analyses were done with the soft corals and also showed that individuals and replicates had no influence on either production or respiration (respectively F=0.15, df:3, p=0.92 in the absence of sediment; F=0.61, df:14, p=0.86 in the presence of sediment for production; F=0.84, df:3, p=0.47 in the absence of sediment; F=0.67, df=14, p=0.81 in the presence of sediment for respiration), proving a homogeneous reaction to experimental conditions in all test animals. In soft corals there were significant differences both in production and respiration between the species (F=14.5, df:4, p=0.0001 for production; F=39.26, df:4, p=0.0001 for respiration, Fig.3b and 4b). A subsequent Tukey test

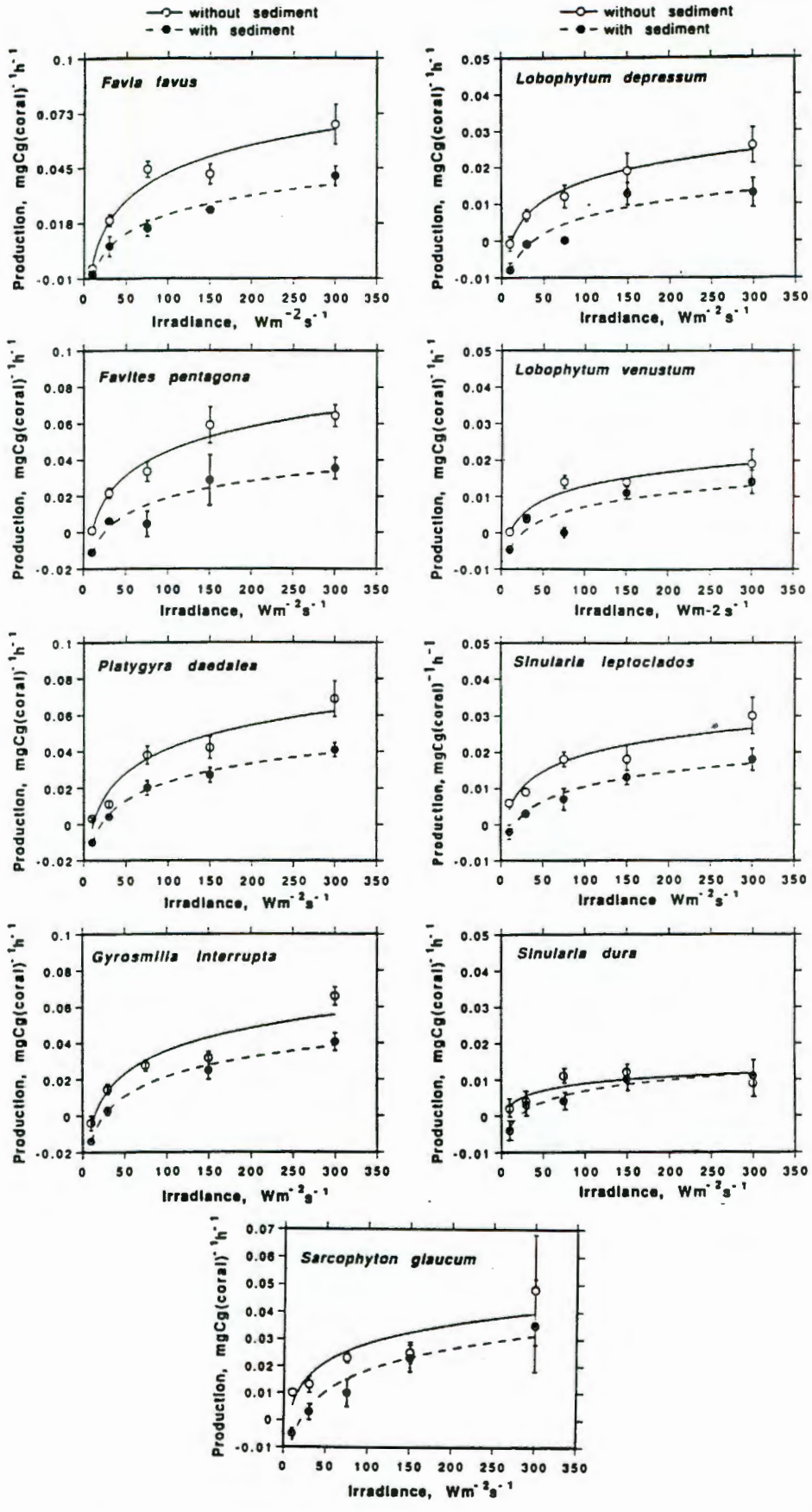


Fig. 3: Irradiance/Production curves for all hard and soft corals without sediment (empty circles, solid line) and with 200mgcm^{-2} sediment applied (filled circles, dashed line). Error bars indicate the standard error.

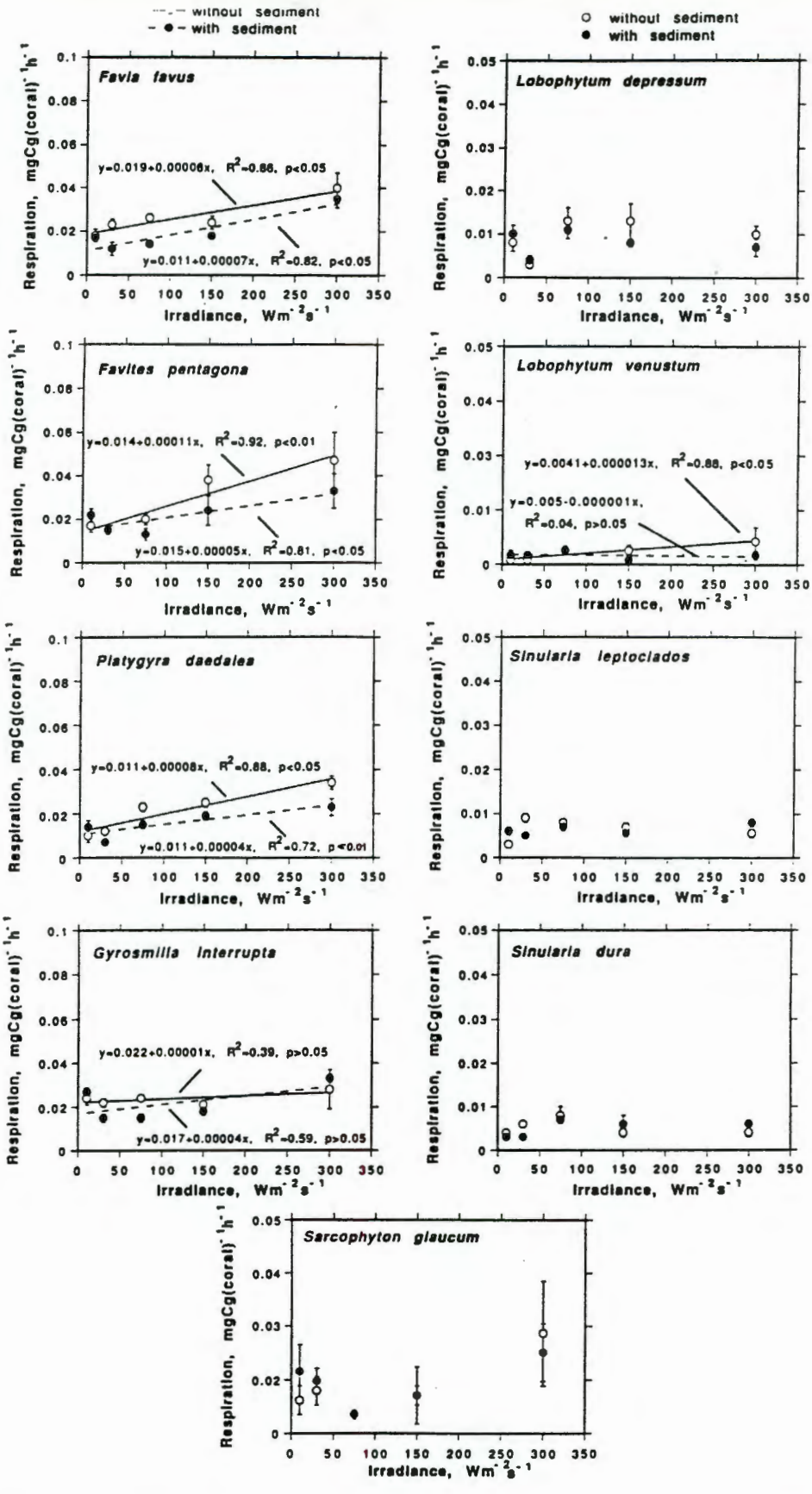


Fig. 4: Irradiance/Respiration relationship for all hard and soft corals without sediment (empty circles, solid line) and with 200mgcm^{-2} sediment applied (filled circles, dashed line). In cases where no regression lines are only given, there existed no correllation. Error bars indicate the standard error.

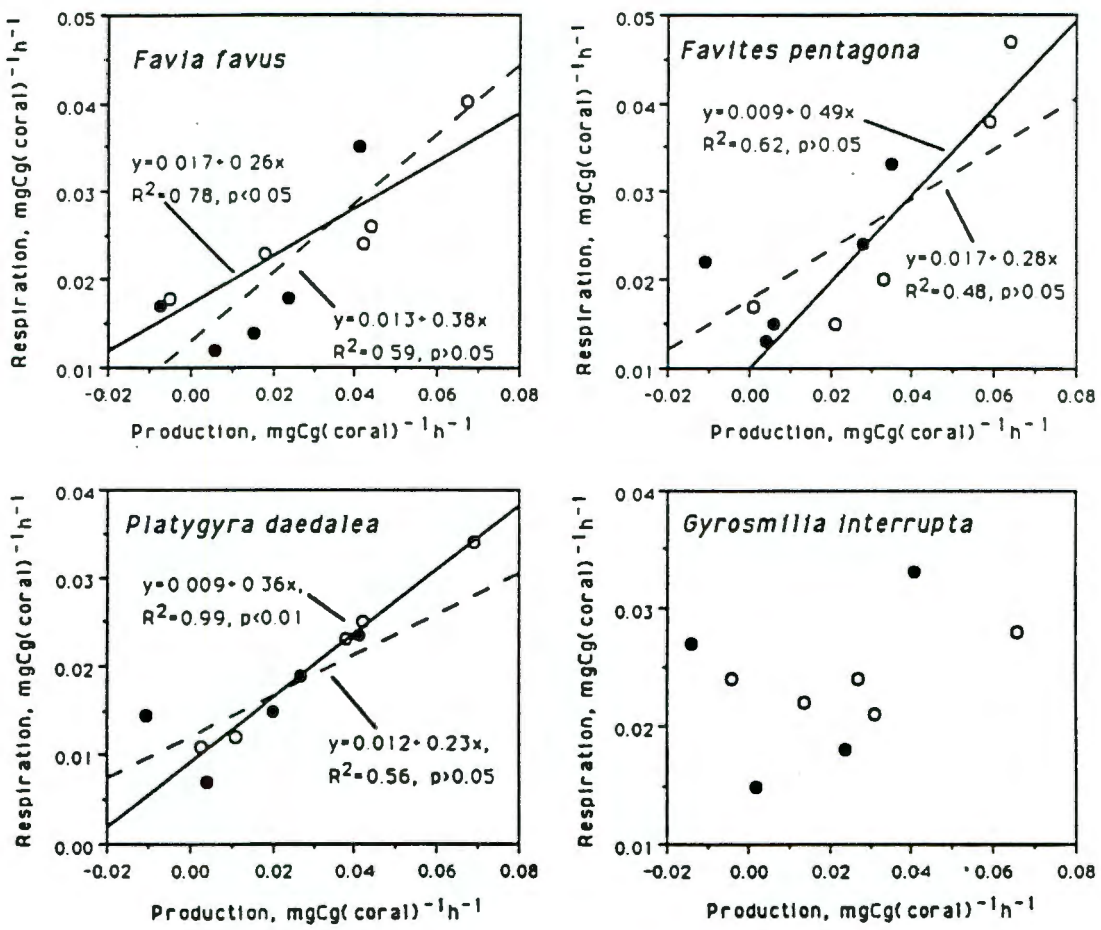


Fig. 5: Relationship between production and respiration in all hard coral species without sediment (empty circles, solid line) and under sediment application (filled circles, dashed lines). Each data point represents a mean value obtained from 6 animals in 5 runs.

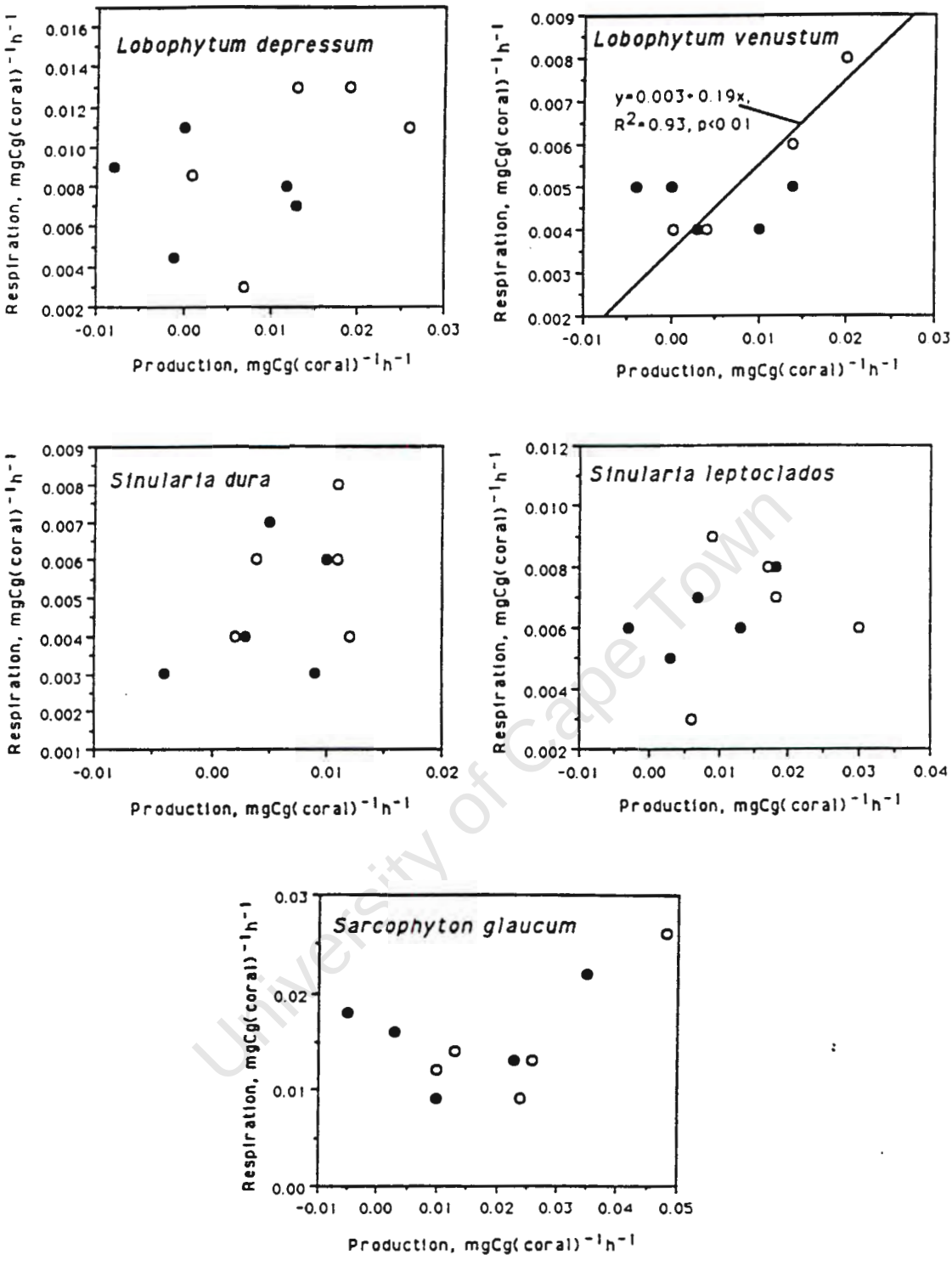


Fig. 7: Relationship between production and respiration in all soft coral species withou sediment (empty circles, solid line) and under sediment application (filled circles, dashed lines). Each data point represents a mean value obtained from 6 animals in 5 runs.

for studentized range showed the differences in production exist between two homogeneous groups of species: L. depressum, L.venustum and S.dura on the one side and S. leptoclados and Sarcophyton glaucum on the other. Only Sarcophyton glaucum differed from all other species in respiration, the other species forming a homogeneous group (Fig. 7). Also when the same analysis was performed seperately for production and respiration data obtained in control- and sedimented conditions, Sarcophyton glaucum, always grouped with the hard corals and not with the soft corals (Fig. 7a & b). Light intensity, the application of sediment and the interaction of both these factors (equally weighed in the analysis) had significant influences on production ($F=56.47$, df:4, $p=0.001$ for light intensity; $F=36.77$, df:1, $p=0.001$ for sediment application; $F=2.62$, df:4, $p=0.034$ for interaction between the previous factors) but not on respiration ($F=1.34$, df:4, $p=0.253$; $F=0.49$, df:1, $p=0.483$). Only the interaction of sand and light had a significant effect on respiration ($F=3.24$, df:4, $p=0.012$).

The P/I-curves of the soft corals were similar to those of the hard corals, except for having lower overall production levels. In Sinularia dura photosaturation appeared to occur at irradiance levels around $150 Wm^{-2}s^{-1}$ (Fig. 3), for all other species it seemed to be in the same region as in the hard corals, slightly above $300 Wm^{-2}s^{-1}$. There was not a similarly marked trend for higher production loss due to sediment application at higher light levels as in the hard corals. Production loss was rather uniform at most light levels in most species (Fig. 3). In Sinularia dura there were greater differences in production at the lower light levels (Fig. 3).

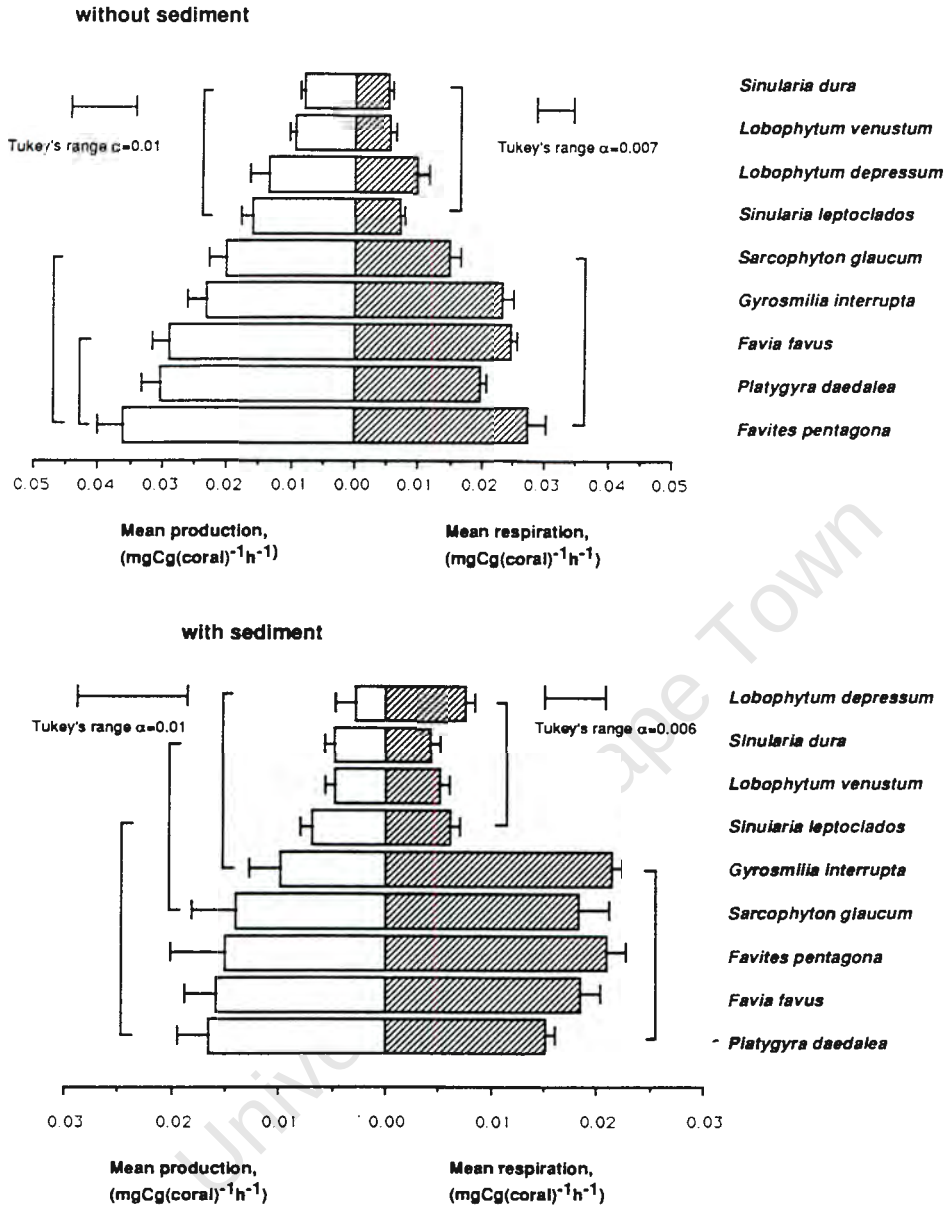


Fig. 7: Differences in total mean production and respiration between all investigated coral species. Significance of differences exists when Tukeys range is smaller than the differences between the upper and lower standard error limits of compared species. Homogeneous groups are indicated by horizontal bars. Note unequal axis length.

Respiration showed no increase with light (Fig. 4), except for unsedimented conditions in Lobophytum venustum. Overall, there were no correlations between production and respiration (Fig. 6). In a separate analysis all hard and soft coral species were compared. The overall model showed significant differences in production and respiration values between the species ($F=27.3$, df:8, $p=0.0001$ for production; $F=73.31$, df:8, $p=0.0001$ for respiration). A subsequent Tukey test for studentized means revealed that two homogeneous species groups existed. One consisting of all hard corals, the other of all soft corals minus Sarcophyton glaucum. This species stood apart in its production and respiration characteristics from all other soft corals and showed some affinities to the hard corals (Fig. 7). Similar to the previous analyses, light levels, the application of sand and the interaction of these two factors had a significant effect on both production and respiration ($F=132.5$, df:4, $p=0.0001$; $F=118.49$, df:1, $p=0.0001$; $F=2.54$, df:4, $p=0.039$ for production; $F=18.83$, df:4, $p=0.0001$; $F=10.47$, df:1, $p=0.0013$; $F=5.39$, df:4, $p=0.0003$) for respiration).

Overall, the results can be summarized as follows. As a starting point, soft corals produced less than hard corals (Figs. 3 & 7). There were no differences in production between the hard coral species, but differences did exist between the soft corals, Sarcophyton glaucum being different from the four other species (Figs. 3&7). In unsedimented conditions, production and respiration were correlated in two hard- and one soft corals (Figs. 5 & 6). In both hard- and soft corals the application of sediment significantly reduced production (Fig. 3). With the

application of sediment (and thus reduced production) respiration also decreased both in hard- and soft corals (Fig. 4). This situation was further investigated in the models.

c) modelling the species responses to sedimentation in different light regimes

As basis for the modeling exercise I used a cloudless Natal mid-winter day, typical of the period in which the experiment was conducted, and the calculated light levels on the reefs as shown in Fig. 1. Total carbon production and respiration were calculated for a best case scenario, assuming only 50% irradiance loss on the community, as could be expected in very clear conditions on a shallow coral community, and an average case scenario, assuming a 75% irradiance loss, as could be expected in murky conditions.

In both scenaria hard corals produced and respired significantly more than soft corals (t-test, t=-4.57, p=0.0025).

All models show clearly that hard corals produce far more carbon per unit tissue than soft corals (figs 8-11).

It is also very clear from the graphs in Figs. 8-11 that serious losses in photosynthetic productivity are suffered due to coverage of the corals by sediment. Losses in hard corals ranged from 37.9% (Gyrosmilia interrupta) to 46% (Favia favus) with an average of 45.1% (±7.6% S.D.) for the 50% PARs scenario (Table 1) and from 43.7% (Platygyra daedalea) to 64.07% (Favites pentagona) with an average of 53.36% (±8.65% S.D.) for the 25% PARs scenario (Table 2). The differences in production loss between the two scenarios were not significant (U-test, z=1.5, p>0.05).

Production losses in soft corals ranged from 29.7% (Lobophytum venustum) to 51.5% (Lobophytum depressum) with an average of37.74%

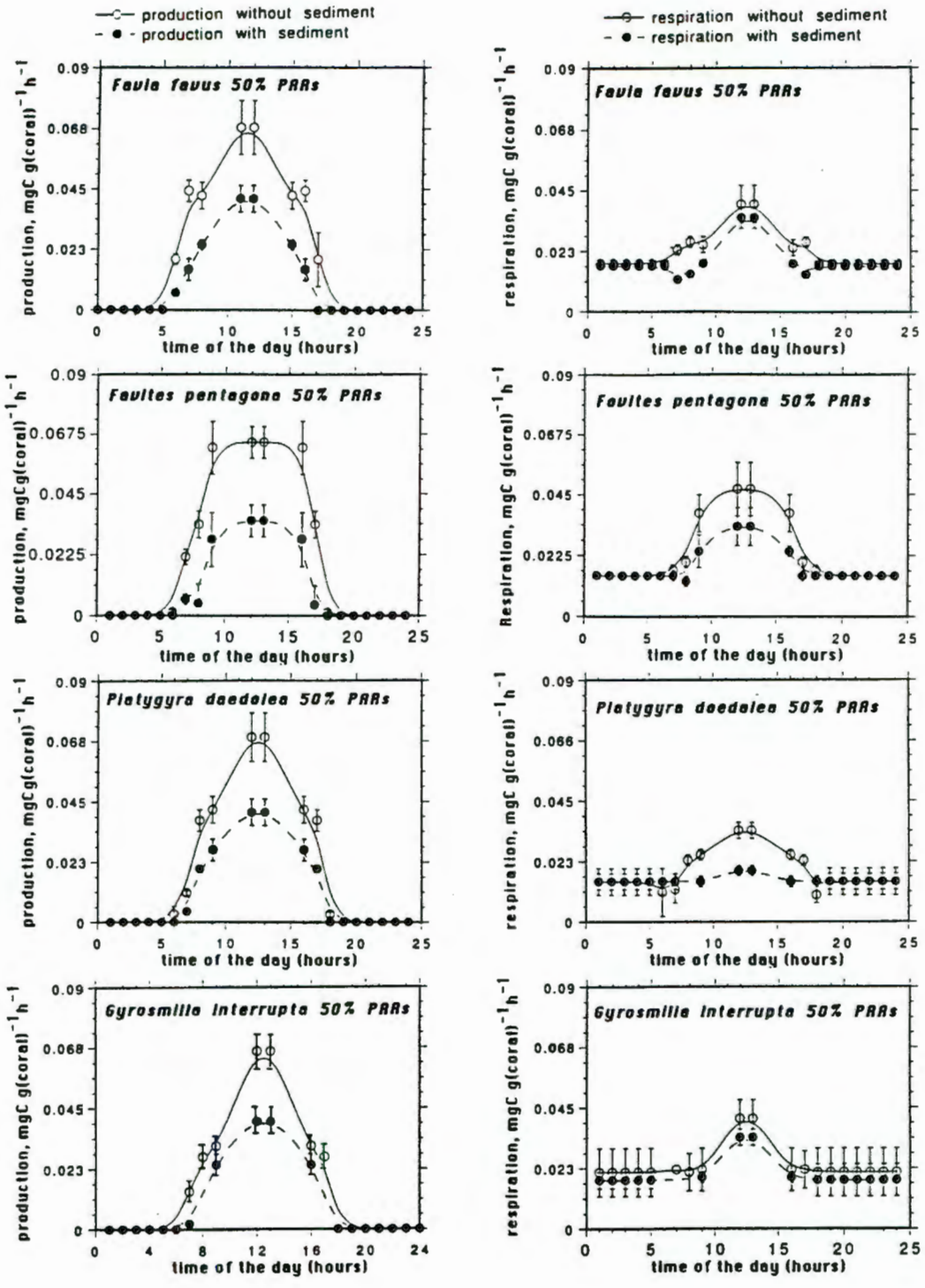


Fig. 8: Models for the effects of sedimentation on daily production and respiration of all hard coral species for the 50% PARs scenario. Irradiance levels pertinent to the production and respiration values for both models can be found in Figure 1. Where no error bars are shown, the error is too small to be drawn (less than 0.001).

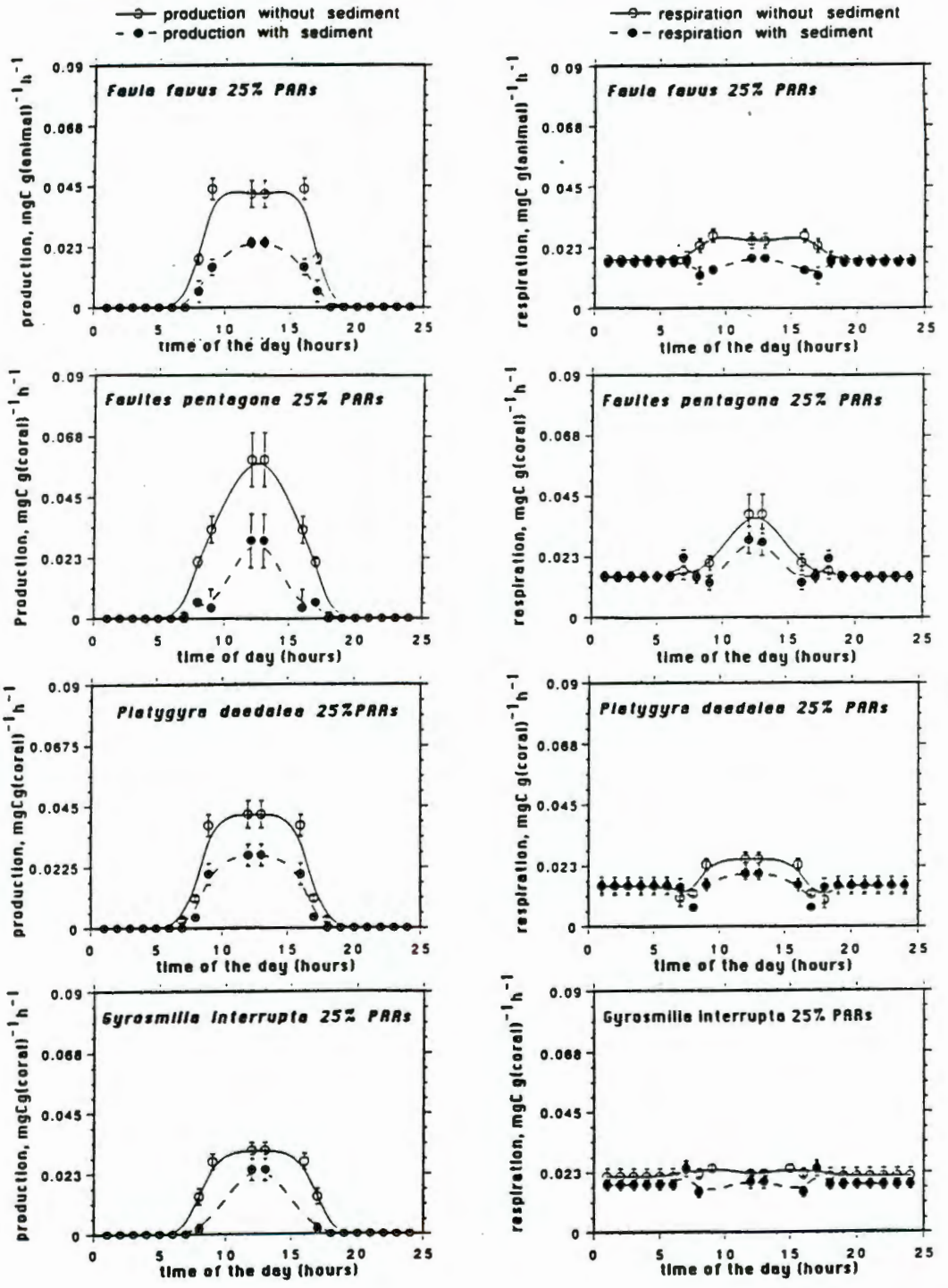


Fig. 9: Models for the effects of sedimentation on daily production and respiration of all hard coral species for the 25% PARs scenario. Irradiance levels pertinent to the production and respiration values for both models can be found in Figure 1. Where no error bars are shown, the error is too small to be drawn (less than 0.001).

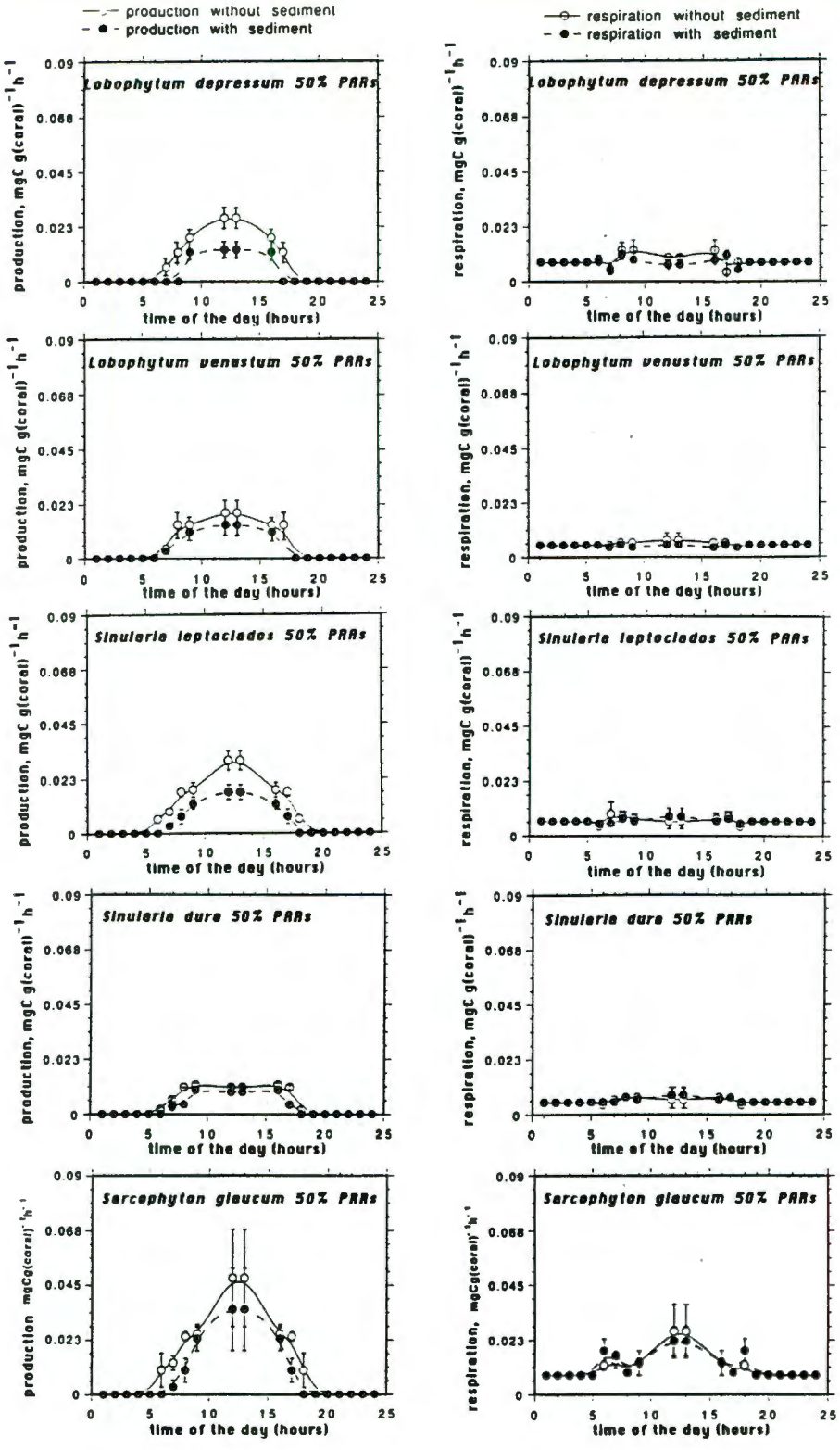


Fig. 10: Models for the effects of sedimentation on daily production and respiration of all soft coral species for the 50% PARs scenario. Irradiance levels pertinent to the production and respiration values for both models can be found in Figure 1. Where no error bars are shown, the error is too small to be drawn (less than 0.001).

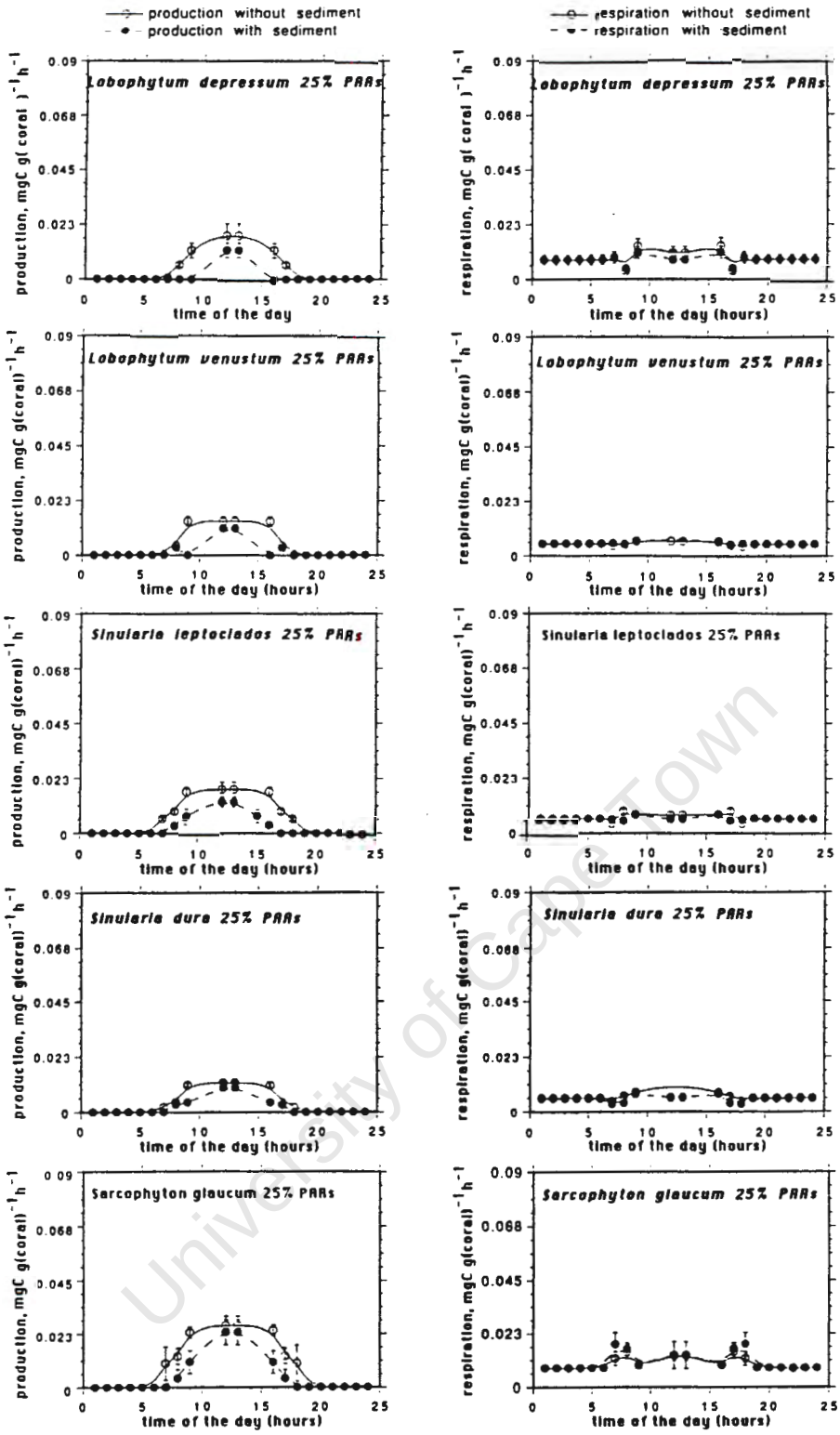


Fig. 11: Models for the effects of sedimentation on daily production and respiration of all soft coral species for the 25% PARs scenario. Irradiance levels pertinent to the production and respiration values for both models can be found in Figure 1. Where no error bars are shown, the error is too small to be drawn (less than 0.001).

24h C-Production & Respiration, 50% PARs

	24h Production no sediment	24h Production with sediment	% P-Reduction with sediment	24h Respiration no sediment	24h Respiration with sediment	% R-Reduction with sediment
F. favus	0.5686	0.2990	46.0	0.5490	0.4580	16.9
F. pentagona	0.5986	0.2686	55.4	0.5790	0.4510	22.1
P. daedalea	0.5370	0.3160	41.1	0.4650	0.3610	22.4
G. interrupta	0.4580	0.2830	37.9	0.5695	0.4840	14.9
L. depressum	0.2060	0.1000	29.7	0.2094	0.1852	11.5
L. venustum	0.1644	0.1155	51.5	0.1280	0.1090	13.3
S. dura	0.1240	0.0870	29.8	0.1300	0.1190	3.7
S. leptoclados	0.2470	0.1330	46.1	0.1400	0.1450	0.0
S. glaucum	0.3730	0.2550	31.6	0.2920	0.2900	0.7

Table 1: Production and respiration characteristics obtained with the 50% PARs model for all corals. Absolute production values are given in $mgCg(coral)^{-1}day^{-1}$.

24h C-Production & Respiration, 25% PARs

	24h Production no sediment	24h Production with sediment	% P-Reduction with sediment	24h Respiration no sediment	24h Respiration with sediment	% R-Reduction with sediment
F. favus	0.3800	0.16800	55.7	0.4872	0.3758	22.9
F. pentagona	0.4120	0.14380	64.1	0.4675	0.4067	12.9
P. daedalea	0.3480	0.19600	43.3	0.4036	0.3514	12.9
G. interrupta	0.2600	0.13000	50.0	0.5050	0.4158	17.6
L. depressum	0.1328	0.04800	63.2	0.2098	0.1910	8.9
L. venustum	0.1204	0.05000	58.2	0.1188	0.1208	1.6
S. dura	0.1040	0.06200	40.4	0.1473	0.1239	15.9
S. leptoclados	0.1700	0.07585	55.3	0.1524	0.1402	8.0
S. glaucum	0.2437	0. 1413	42.0	0.2298	0.2468	6.8

Table 2: Production and respiration characteristics obtained with the 25% PARs model for all corals. Absolute production values are given in $mgCg(coral)^{-1}day^{-1}$.

(±10.29% S.D.) for the 50% PARs scenario (Table 1) and from 40.4% (Sarcophyton glaucum) to 63.25% (Lobophytum depressum) with an average of 51.88 (±10.17% S.D.) for the 25% PARs scenario (Table 2). The differences between the proportional losses for the two scenarios were not significant (U-test, z=0.89, p=0.07).

Overall decreases in respiration were also observed. They ranged in hard corals from 14.9% (Gyrosmilia interrupta) to 22.4% (Platygyra daedalea) with an average of 19.1 (±3.7% S.D.) for the 50% PARs scenario (Table 1) and from 12.9% (Favites pentagona and Platygyra daedalea) to 22.8% (Favia favus) with an average of 16.5 (±4.7% S.D.) for the 25% PARs scenario (Table 2). The differences between the proportional losses for two models were not significant (U-test, z=-0.5, p=0.61). In the soft corals respiratory decreases under sedimentation ranged from 0% (Sinularia leptoclados, Sarcophyton glaucum) to 13.3% (Lobophytum venustum) with an average of 5.82 (±6.16% S.D.) for the 50% PARs scenario (Table 1). In the 25% scenario respiratory increase by 1.6% was observed in Lobophytum venustum and by 6.8% in Sarcophyton glaucum. The other three species showed respiratory decrease by an average of 10.85 (±4.1% S.D.; Table 2). There were no significent differences in the percentage respiratory decreases between the two models (U-test, z=1.7, p=0.07). The decreases in respiration were however not as high as those in production (Table 1). Therefore the proportional C-loss due to respiration increased under sedimentation.

P/R ratios calculated for maximum irradiance at noon showed that under these conditions all species were autotrophic both with and without sediment cover in the 50% PARs as well as the 25% PARs model. In the absence of sediment cover, and with 50% PARs, P/R

	24h P/R Ratio 50% PARs without sediment	24h P/R Ratio 50% PARs with sediment	Noon P/R Ratio 50% PARs without sediment	Noon P/R Ratio 50% PARs with sediment	24h P/R Ratio 25% PARs without sediment	24h P/R Ratio 25% PARs with sediment	Noon P/R Ratio 25% PARs without sediment	Noon P/R Ratio 25% PARs with sediment
Favia favus	1.03	0.65	1.67	1.17	0.78	0.48	1.45	1.33
F.pentagona	1.03	0.59	1.36	1.06	0.88	0.35	1.55	1.21
P. daedalea	1.17	0.87	2.02	1.78	0.86	0.56	1.72	1.42
G. interrupta	0.80	0.58	2.27	1.19	0.51	0.31	1.47	1.33
L. depressum	0.98	0.53	2.60	1.85	0.63	0.25	1.38	1.50
L. venustum	1.28	1.05	2.71	2.80	1.01	0.41	2.33	2.75
S. dura	0.95	0.73	1.83	3.00	0.71	0.50	3.00	2.00
S. leptoclados	1.70	0.90	5.35	2.20	1.11	0.54	2.57	2.40
Sarco. glaucum	1.27	0.87	1.85	1.59	1.06	0.57	1.92	1.77

Table 3: P/R values for the entire 24h period of a modelled day and for noon-time maximum irradiance in the 50% PARs model and the 25% PARs model.

ratios over 24 hours showed three species (Gyrosmilia interrupta, Lobophyton depressum, Sinularia dura) to be heterotrophs, although they had a P/R ratio only slightly below 1. Under sediment and with 50% PARs, all but one of the species (Lobophytum venustum) had P/R ratios well below 1. In the 25% PARs model only two species (Lobophytum venustum, Sinularia leptoclados) had P/R ratios above 1 in the model without sediment interference. With sediment interference all species were below 1 (Table 3).

d) Carbon loss due to mucus production

The results from the mucus measurements are summarized in Table 4. Overall, hard corals, except Platygyra daedalea, produced more mucus than the two soft coral species that were tested. The percentage of respired carbon allocated to mucus production was however lower in the hard corals, as their overall respiration was much higher than in the soft corals (Table 4).

With sediment application the mucus production increased in all corals except Platygyra daedalea. The differences between the percentage of C lost to mucus production in sedimented and unsedimented conditions were significant for all investigated species (U-test, $z=2.041$, $p=0.041$), C-loss due to increased mucus production being higher in sedimented conditions.

In the absence of sediment, mucus production accounted for the lowest share of daily respiration in Platygyra daedalea (15.7%), the highest in Lobophytum venustum (74.2%). When sediment was applied, the lowest percentage was again in Platygyra daedalea (16.5%), the highest in Sinularia leptoclados (91.1%, Table 4).

When C-loss due to mucus production was compared using the total daily production and respiration rates calculated for the two

24h mucus production

	24h mucus P no sediment	% 24h R no sediment	% 24h P no sediment	24h mucus P with sediment	% 24h R with sediment	% 24h P with sediment	mucus sheet with sediment	% 24h P mucus sheet
F. favus	0.1889	34.4	33.20	0.2970	65.13	176.8	0.170	56.0
F. pentagona	0.1559	26.9	26.06	0.3244	71.92	121.0	0.800	300.0
P. daedalea	0.0733	15.7	13.60	0.0596	16.50	18.9	0.600	189.9
G. interrupta	0.1224	21.5	26.84	0.2550	52.70	90.1	0.400	141.3
L. verrustum	0.0950	74.2	57.80	0.0992	91.10	85.9	0.210	181.8
S. dura	0.0616	47.3	49.70	0.0980	82.30	264.8	0.125	337.8

Table 4: Mucus production (mucus P) and the proportional loss of produced (% 24h P) or respired (% 24h R) Carbon due to mucus production under sedimented and unsedimented conditions. Absolute values of mucus production are given in $mgCg(coral)^{-1}day^{-1}$. Mucus sheet refers to the entire amount of mucus trapped with the sediment removed from the corals' surface.

models (50% PARs and 25% PARs), the proportional differences in the share of C-loss due to mucus production of daily respiration and net production were not significant (U-test, z=1.21, p=0.22 for respiration and production respectively).

Carbon content of the total mucus adhering to the sediment was very high and accounted in most species for more than a full days production ranging from only half a day's net production in Favia favus to 3.5 days worth of net production in Sinularia dura (Table 4).

Discussion

The results of this study and the modelling exercise show clearly how profound an influence sedimentation exerts on the energetic balance of hermatypic hard and soft reef corals. This is due to the sediment's ability to absorb or reflect light and to stimulate increased mucus production. Both these factors cause shifts in the coral's energy balance, which lead to a decreased energy input by algal production and an increased energy export by stepped-up mucus production. Although significant differences existed between the production and respiration values of the hard and the soft corals (soft corals produced and respired much less per unit tissue than hard corals), their immediate energetic reactions to sedimentation was roughly the same as in the hard corals, i.e. loss in production and respiration. However, unlike the hard corals, soft corals showed little active behaviour to rid themselves of sediment, other than inflation of the entire corallum and the formation of mucus sheets (see following chapter).

The relative similarity of the different corals' reactions, despite varying baseline production and respiration, allowed construction of a generalized scheme of the physiological response of corals to sedimentation. Fig. 12 is a conceptual diagram explaining the dynamics of sediment/coral interaction. It is based on the results from the 50% PARs model (Figs. 8 & 10) and the 25% PARs model (Figs. 9 & 11). The models assume a constant output of mucus over the day (Crossland et al., 1980). In normal conditions a high proportion of ambient light (vertical arrows) reaches the zooxanthellae (indicated as black dots), which photosynthetically produce carbon. Animal and algal respiration together accounted for about 90% of the daily net production. Of the total respiration approximately 35% was used for mucus production, while about 65% could be used for other metabolic requirements. Under the tested sedimentation conditions (200 $mgcm^{-2}$) the situation changed dramatically. Only about 25% of ambient light reached the zooxanthellae, which were thus only able to produce photosynthetically only about half of the production reached under control conditions. Respiration accounted for about 130% of the daily production and 65% of the total respiration was allocated to mucus production but only 35% to general metabolic requirements. The increased respiration (relative to production) and the productivity loss due to reduction of light pushed the P/R ratios of all but one coral species (Lobophytum venustum) below 1, indicating a situation where photosynthesis produces less carbon than is respired. The fact that Lobophytum venustum still had a positive C-balance can be explained by its growth form. Numerous high ridges on the coral's upper surface create a large proportion of surface that cannot be covered by sediment and therefore did

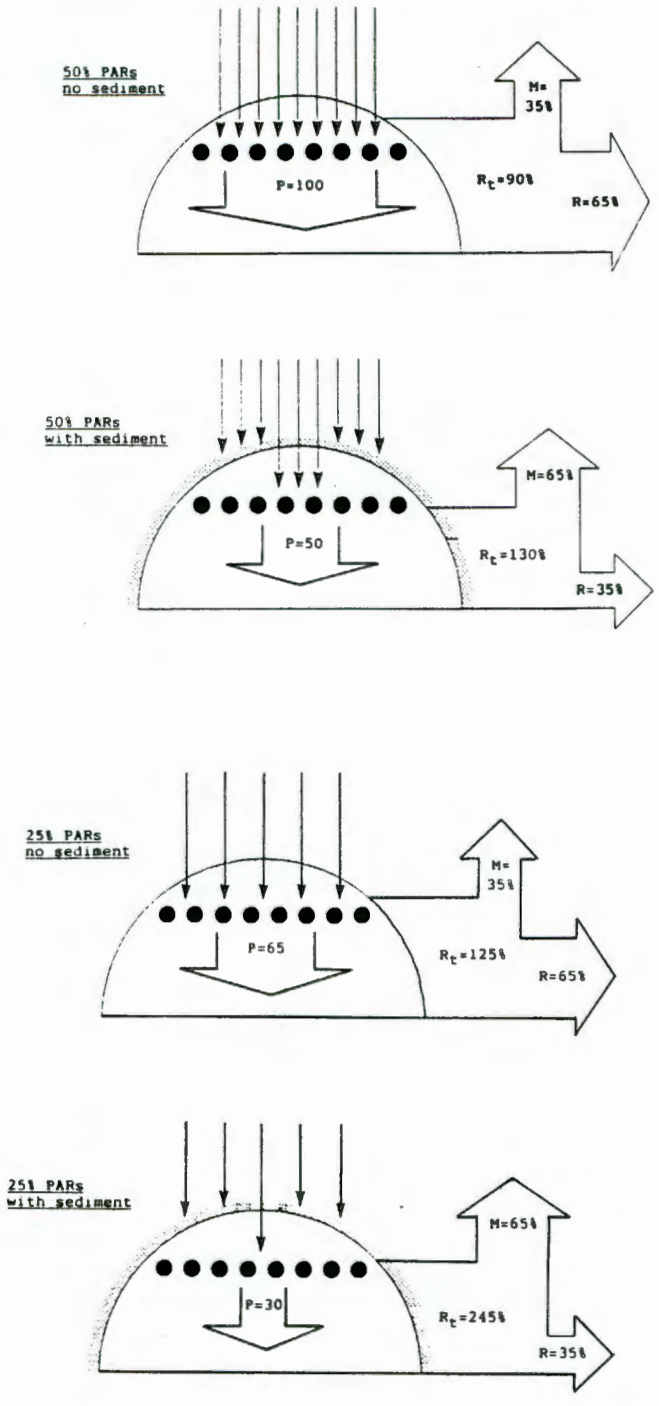


Fig. 12: Conceptual model of the influence of sediment on coral energy budgets. Vertical arrows indicate ambient light levels. Black dots indicate zooxanthellae. Shading on the outside of semicircle indicates sediment. P=Production. Production values are percentages of average maximum production obtained in the 50% PARs model. R_t= total respiration, expressed as percentage of the production inside the stylized coral. M= percentage of respired C lost to mucus, R= percentage of respired C used for other metabolic requirements. Both expressed as percentage of R_t.

not suffer any losses in photosynthetic production. This showes the importance of coral morphology on countering harmful effects of sedimentation (see previous chapter; Stafford-Smith, 1993).

In the 25% PARs model the energetic starting point for most corals was already in the heterotrophic domain at P/R ratios well below 1 (Table 3). Again, as in the previous model, overall metabolic activity decreased with sediment application, while the proportional share of respiration in production doubled. In this model corals respired roughly 2.5 times the amount of C than they produced in 24h.

It is obvious that such a situation is most unfavourable for the organism's fitness. Sedimentation, however, not only interferes with the coral's energy balance by forcing respiratory losses up and photosynthetic production down, it also renders heterotrophic energy gain by prey capture difficult by interfering with the prey capturing apparatus. This may however be of lesser importance, as symbiontic corals are believed to be less efficient prey-catchers due to morphological adaptations for harbouring zooxanthellae (Wilkinson et. al, 1988). Under heavily sedimented conditions the corals therefore seem to shut down most of their normal metabolic functions in order to produce large quantities of mucus, which seems to aid sediment removal (Bak & Elgershuizen, 1976; Coffroth, 1988; Stafford-Smith & Ormond, 1992). The practice of producing mucus sheets (Coffroth, 1988; Stafford-Smith & Ormond, 1992) appeared in the present study to be an extremely costly way of reacting to the environment, as in most cases carbon equivalent to several days of production was found in mucus adhering to sediment (Table 4). It seems very likely that over longer periods of time this situation is bound to create severe problems for the corals

and may very well explain reported long-term changes in physiology (Szmant-Froelich et al., 1981) and damage to coral tissue by continued sedimentation (Peters & Pilson, 1985; Rogers, 1990; Stafford-Smith & Ormond, 1992). In the next chapter I investigate the effects of long-term sedimentation on hard- and soft corals.

The diagrams also illustrate another finding. While the share of respiration in production increases under sedimentation, the total respiration in sedimented conditions is much lower than in unsedimented conditions. It is also interesting to note that while production values showed the expected saturation curve (Barnes & Chalker, 1990; Falkowski et al., 1990), respiration did not follow this trend but showed a linear increase with increasing light levels in some hard- and soft corals and at least a tendency to increase in the other hard- and soft corals (Figs. 3 & 4). Similar results were reported by Titlyanov (1991), who observed increased respiration over the peak production period in a 24h cycle in Pocillopora damicornis. It is conceivable that photodynamic effects (Schick & Dykens, 1985) play a role in increasing respiration values, while net production stagnates. The photosynthetically produced oxygen is toxic in hyperbaric conditions (Dykens & Schick, 1984; Schick & Dykens, 1985), which are achieved under maximum production. The corals therefore have to counteract these effects by enzymatic activity (Dykens & Schick, 1984; Schick & Dykens, 1985). It is possible that the increased enzyme production in higher light levels is one of the causes of increased respiration, while production might stagnate due to photodynamic processes (Falkowski et al. 1990).

The production modelling exercise and mucus analysis showed that while the influence of sedimentation on corals is comparable under

different ambient light levels, corals living in lower light levels may be more adversely affected than corals living in a better lit environment. The little light that is available, gets even further reduced by the layer of sediment on the coral. Furthermore, the proportional increase in respiration was found to be higher in poorly-lit than in better-lit conditions. The 25% PARs model showed most corals to be heterotrophic over 24h. Therefore a layer of sediment on the animals, which would also interfere with prey capture, has a negative influence on energy uptake.

On South African coral reefs, shallow communities are dominated in wide areas by the soft corals Lobophytum patulum, Sinularia leptoclados and other species with similar morphology. This study has shown that these corals lose less productivity under sedimented conditions, due to their morphology. This may give them enough advantage to outgrow most other competitors with a less advantageous growth form.

Conclusion

The present models for the energy balance of hard and soft corals under sedimented and unsedimented conditions show that sedimentation has severe effects on the energy budgets of all species. Sedimentation causes a loss of available light, which leads to decreased C-production by photosynthesis. Overall respiration was found to decrease in accordance with production, but the proportional share of respiration increased, resulting in P/R ratios lower than 1 in almost all species in both models. Mucus production proved to be an important C-sink for the coral, especially under sediment stress when the C-requirements for

stepped-up mucus production more than doubled. Mucus adhering to cleared-off sediment amounted (in terms of C-content) to between one half and several days worth of production. This leads to the assumption, that mucus sheets, as commonly used by corals as defence against sedimentation, are metabolically very expensive.

Literature cited:

Abdel-Salam, H. & J.W. Porter. 1988. Physiological effects of sediment rejection on photosynthesis and respiration in three caribbean reef corals. Proc. 6th Int. Coral Reef Symposium, Australia, 1988: 285-292.

Bak, R.P.M. & J.H.B.W. Elgershuizen. 1976. Patterns of oil-sediment rejection in corals. Mar.Biol. 37: 105-113.

Barnes, D.J. & B.E. Chalker. 1990. Calcification and photosynthesis in reef-building corals and algae. in: Dubinsky, Z. (ed.): Coral Reefs-Ecosystems of the world 25; Elsevier Amsterdam-New York: 109-131.

Beckley L.E. & R.C. Van Ballegooyen. 1992. Oceanographic conditions during three ichthyoplankton surveys of the Agulhas current in 1990/91. S.Afr.J.mar.Sci. 12: 83-93.

Benson, A.A. & L. Muscatine. 1974. Wax in coral mucus: energy transfer from corals to reef fishes. Limnol.Oceanogr.19(5): 810-814.

Coffroth, M.A. 1988. The function and fate of mucous sheets produced by reef coelenterates. Proc. 6th Int.Voral Reef Symp., Australia, Vol.2: 15-19.

Crossland, C.J., D.J. Barnes & M.A. Borowitzka. 1980. Diurnal lipid and mucus production in the staghorn coral Acropora acuminata. Mar.Biol. 60: 81-90.

Dai, C.F. 1991. Distribution and adaptive strategies of alcyonacean corals in Nanwan Bay, Taiwan. Hydrobiologia 216/217: 241-246.

Dallmeyer, D.G., J.W. Porter & G.J. Smith. 1982. Effects of particulate peat on the behaviour and physiology of the Jamaican reef-building coral Montastrea annularis. Mar.Biol. 68: 229-233.

Dinesen, Z.D. 1983. Patterns in the distribution of soft corals across the central Great Barrier Reef. Coral Reefs 1: 229-236.

Done, T.J. 1983. Patterns in the distribution of coral communities across the Great Barrier Reef. Coral Reefs 1: 95-107.

Dykens, J.A. & J.M. Schick. Photobiology of the symbiotic sea anemone Anthopleura elegantissima: defenses against photodynamic effects, and seasonal photoacclimatisation. Biol.Bull. 167: 683-697.

Falkowski, P.G., P.L. Jokiel & R.A. Kinzie III. 1990. Irradiance and corals. in: Dubinsky, Z. (ed.): Coral Reefs-Ecosystems of the world 25; Elsevier Amsterdam-New York: 89-107.

Herndl, G.J. & B. Velimirov (1986). Microheterotrophic utilization of mucus released by the mediterranean coral Cladocora caespitosa. Mar.Biol. 90: 363-369.

Laboute, P. 1988. The presence of scleractinian corals and their means of adapting to a muddy environment: the "Gail Bank". Proc. 6th Int. Coral Reef Symposium, Australia, Vol.3: 107-111.

Lasker, H.R. 1980. Sediment rejection by reef corals: the roles of behavior and morphology in Montastrea cavernosa (Linnaeus). J.Exp.mar.Biol.Ecol. 47: 77-87.

Peters, E.C. & M.E.Q. Pilson. 1985. A comparative study of the effects of sedimentation on symbiotic and asymbiotic colonies

of the coral Astrangia danae Milne-Edwards and Haime 1849. J.Exp.Mar.Biol.Ecol.92: 215-230.

Richman, S., Y. Loya & L.B. Slobodkin. 1975. The rate of mucus production by corals and its assimilation by the coral reef copepod Acartia negligens. Limnol.Oceanogr.20(6): 918-923.

Rice, S.A. & C.L. Hunter. 1992. Effects of suspended sediment and burial on scleractinian corals from west central Florida patch reefs. Bull.Mar.Sci. 51(3): 439-442.

Rogers, C.S. 1990. Responses of coral reefs and reef organisms to sedimentation. Mar.Ecol.Progr.Ser. 62: 185-202.

Rogers, C.S. 1983. Sublethal and lethal effects of sediments applied to common caribbean reef corals in the field. Mar. Poll.Bull. 14(10): 378-382.

Shick, J.M. & J.A. Dykens. 1985. Oxygen detoxification in algal-invertebrate symbioses from the Great Barrier Reef. Oecologia(Berlin) 66: 33-41.

Schuhmann, E.H. 1988. Physical oceanography off Natal. In: Coastal Ocean studies off Natal, South Africa. Schuhmann, E.H. (ed.) Berlin Springer: 101-130 (Lecture Notes on Coastal and Estuarine Studies 26).

Spencer-Davies, P. 1991. Effect of daylight variation on the energy budgets of shallow-water corals. Mar.Biol. 108: 137-144.

Stafford-Smith, M.G. & R.F.G. Ormond. 1992. Sediment-rejection mechanisms of 42 species of Australian scleractian corals. Aust.J.Mar.Freshwater Res. 43: 683-705.

Stafford-Smith, M.G. 1993. Sediment-rejection efficiency of 22 species of Australian scleractinian corals. Mar.Biol. 115: 229-243.

Strickland, J.D.H. & T.R. Parson. 1972. A practical handbook of seawater analysis, 2nd ed. Bull.Fish.Res.Bd.Can. 167: 1-310.

Szmant-Froelich, S., Johnson, V. & T. Hoehn. 1981. The physiological effects of oil-drilling muds on the caribbean coral Montastrea annularis. Proc. 4th Int. Coral Reef Symposium, Manila, Vol.1: 163-168.

Titlyanov, E.A. 1991. The stable level of coral primary production in a wide light range. Hydrobiologia 216/217: 383-387.

Wilkinson, C.R., A.C. Cheshire, D.W. Klumpp & D.A. McKinnon. 1988. Nutritional spectrum of animals with photosynthetic symbionts-corals and sponges. Proc. 6th Int. Coral Reef Symp., Australia, Vol. 3: 27-30.

Yamasu, T. & S. Mizofuchi. 1989. Effects of synthetic, neutral detergent and red clay on short term measurements of O_2 production in an Okinawan reef coral. Galaxea 8, 127-42.

EFFECTS OF SHORT- AND LONG TERM SEDIMENTATION ON SOUTH AFRICAN HARD- AND SOFT CORALS

Abstract

The effects of experimentally induced sedimentation on a short term (17 hours) and a long-term (6 weeks) basis were investigated in four hard coral species (Favia favus, Favites pentagona, Platygyra daedalea, Gyrosmilia interrupta) and five soft coral species (Lobophytum depressum, L. venustum, Sinularia dura, S. leptoclados, Sarcophyton glaucum) from South Africa. Additional short-term experiments were conducted on another four hard coral species (Galaxea fascicularis, Cyphastrea chalcidicum, Favites abdita, Goniopora djiboutensis). Hard corals were found to be very active in clearing sediment from their surface, while soft corals exhibited much less success in clearing their entire surface. The efficiency of short-term sediment clearing in hard corals was dependent primarily on the shape of the corallum. The usual reaction to sediment application was hydrostatic inflation of the polyps in hard corals and of the entire corallum in soft corals. Increased tentacular action was observed in Gyrosmilia interrupta, a species unable to inflate its polyps to the same extent as the other species. Long-term sedimentation lead to exhaustion and reduced behavioural response of the corals. Inflation of polyps or the corallum remained the same through the entire course of the experiment, while other activities, such as tentacular activities, ceased completely. In hard and soft corals, tissue necroses appeared within the first week of long-term sediment application. Death of entire colonies due to sedimentation was observed in soft corals but not in hard corals. Soft corals lost significantly more weight under sedimented than under control conditions. In soft corals partial bleaching of continually covered areas was observed. Different grain sizes of sand had no influence on clearing reaction or efficiencies. The different reactions of hard and soft corals to long-term sedimentation are used to interpret community patterns on South African reefs.

Introduction

It is a well established fact that sedimentation is an important factor controlling coral growth and thus reef development (Hubbard, 1986; Rogers, 1990). Sedimentation can interfere with corals directly, by influencing growth rates (Hubbard & Scaturo, 1985), metabolism (Dallmeyer et al., 1982; Abdel-Salam & Porter, 1988; Edmunds & Davies, 1989, see next chapter) and fecundity (Tomascik & Sander, 1987), as well as by causing histopathological damage (Peters & Pilson, 1985); it can also interfere at population level by either reducing or facilitating larval settlement (Rogers et al., 1984; Wittenberg & Hunte, 1992).

Corals have developed various defence mechanisms to sedimentation. Hard corals can reject sediment to a certain degree by means of morphological adaptations and by directed behaviour (Hubbard & Pocock, 1972; Bak & Elgershuizen, 1976; Lasker, 1980; Stafford-Smith & Ormond, 1992; Stafford-Smith, 1993), soft corals have however been neglected in such studies and only circumstantial evidence exists of their ability to withstand sedimentation (Dinesen, 1983; Dai, 1991). On South African reefs, however, they form a significant proportion of the coral community and are dominant over wide areas. I have previously speculated that sedimentation may be a key factor influencing South African coral communities (see Part II), resulting in differential dominance of hard and soft corals in areas of different sedimentation. In order to verify these speculations, it is of importance to know whether hard and soft corals react differently to sedimentation.

The aims of the present study were: 1) to establish if there are differences in the mechanisms employed by hard and soft corals in removing sediment; 2) to evaluate differences in the corals'

reaction to short-term and long-term sedimentation; 3) to correlate the observed reactions of the different species with community structure on South African reefs (see Part II).

Material and methods

All experiments were conducted in the laboratory, as strictly regulated conditions were desired. The experimental corals were split into two groups. Nine species were used for the entire experimental period, as enough replicates (n=8) were available for these species (the hard corals Favia favus, Favites pentagona, Platygyra daedalea, Gyrosmilia interrupta and the soft corals Lobophytum depressum, Lobophytum venustum, Sinularia dura, Sinularia leptoclados, Sarcophyton glaucum). A second group of corals was also used in parts of the experiment (Galaxea fascicularis, Cyphastrea chalcidicum, Favites abdita, Goniopora djiboutensis) in order to provide additional data. However, only a single specimen of each of these species was available. While this severe limitation precluded any statements on species-specific responses of these species to sedimentation, the data obtained from these corals could still be used as additional data-points characterizing the responses of certain growth-form-types.

All corals were collected on the Maputaland reef systems in northern Natal and transported by truck in a 500 litre container with sea water slightly hypersaturated with medical oxygen to Durban. There they were kept in flow-through tanks with well-point sea-water at light levels roughly comparable to their natural habitat. All the species were common and considered indicators (see Part II) for either high sedimentation (F. favus, F. pentagona, L. depressum, S. dura) or low sedimentation

environments (L. venustum, S. leptoclados), although two species (G. interrupta, P. daedalea) did not show any preference for either of these environments. Eight specimens of each species were used in the experiments. The animals were fed twice a week with rotifers and brine-shrimp nauplii (Peters & Pilson, 1985) to avoid starvation, in case heterotrophic energy uptake was necessary. Under the experimental light conditions, however, all animals were autotrophic under the controlled control conditions (light levels were held at 50% PARs, see preceding chapter for rationale).

The short-term sedimentation experiment

The sediment used was locally collected sand. Three batches were used to test for diffential reaction to the different grain sizes of fine (average grain size=0.129mm), medium (average grain size=0.253mm) and coarse sand (average grain size=0.699mm). The effect of grain size was tested for all hard corals but only for two soft coral species (Lobophytum venustum, Sarcophyton glaucum). The sediment was applied to the corals through a funnel, which ensured that all sediment landed on them. It was applied to provide a continuous cover of 200mgcm^{-2}, this being the dose used in all studies during the sedimentation experiment (see previous chapter). The rejected sediment was collected in trays positioned under the corals and collected after 10, 100 and 1000 minutes. It was filtered through a sieve of 0.04 mm mesh, air dried and weighed. After 1000 minutes all sediment remaining on the corals was removed and weighed. The measurements thus obtained were clearing rate (the amount of sediment cleared off the corals, expressed as gmin^{-1}) and clearance efficiency (the proportion of sediment removed at the end of the experimental period). The animals were allowed to rest for 8 hours before another load of

sediment was applied. When collecting the trays, the condition of the corals was noted, e.g. whether polyps were inflated, tentacles extended, mucuous sheets apparent, or mesenterial filaments extruded. The behaviour of control animal was observed simulataneously.

The long-term sedimentation experiment

To test for the corals' reaction to continuous sedimentation, a long-term experiment was set up. Three to five specimens of each species were placed in adjacent tanks, one for control conditions and one for sedimented conditions. Care was taken to avoid putting the animals into physical contact, as this could have resulted in aggressive reactions and tissue damage due to tentacular action, which could have distorted results. A constant flow of sediment onto the experimental corals was maintained for six weeks by means of a recirculatory system as illustrated in Fig. 1. The sediment cover on the corals was maintained at roughly 200 $mgcm^{-2}$, this being the amount of sediment being used in parallel physiological experiments (see previous chapter) and a level of sedimentation corresponding well to that observed on the reefs (see Part II).

At weekly intervals the corals of the control and experimental groups were weighed and their volume was determined by means of water displacement. Soft corals were squeezed dry with a water absorbant cloth until no more water could be drawn. This procedure was necessary, as soft corals can hold varying degrees of water, which would distort results. During the weighing procedure care was taken not to damage the animals. Hard corals could not be weighed as live tissue only made up a small fraction of the total weight (skeleton+soft tissue) and the changes in weight due to necroses were not measured accurately by the balance.

Description of colony morphology

As all specimens had a massive, more or less rounded growth form, it was necessary to describe their morphology in standardized terms. Their degree of sphericity, i.e. how closely they approached a hemisphere, was expressed by a simple height/diameter ratio, similar to that formulated by Lasker (1980):

I_S=maximal height/maximal diameter

which is 0.5 for a hemisphere (the smaller the index, the flatter the corallum). This index was not used for soft corals, which had either a completely flat surface (L. depressum, S. dura) or a very complicated surface, with numerous ridges or finger-like projections (L. venustum, S. leptoclados). In these cases the index would not have made sense and was not used.

Also a meandrization index, as formulated by Veron et al. (1977) was used to describe the degree of fusion of individual corallites into longer series (also referred to as "valleys").

I_m=number of centres/numbers of valleys

The higher the value, the longer the valleys. Monocentric species have an I_m of 1.

Chlorophyll analysis

Chlorophyll was extracted by means of hot methanol extraction (HMSO, 1986) from tissue blocks of $5mm^3$ taken from different parts of the experimental colonies. Optical densities were read at 664, 647 and 630nm and converted to concentration of total chlorophyll (a, b and c) using the formula derived by Jeffrey & Humphrey (1975).

$$21.78\ (OD_{630})+11.89\ (OD_{647})+4.75\ (OD_{664})=\text{ug chlorophyll}$$

Description of colony morphology

As all specimens had a massive, more or less rounded growth form, it was necessary to describe their morphology in standardized terms. Their degree of sphericity, i.e. how closely they approached a hemisphere, was expressed by a simple height/diameter ratio, similar to that formulated by Lasker (1980):

I_S=maximal height/maximal diameter

which is 0.5 for a hemisphere (the smaller the index, the flatter the corallum). This index was not used for soft corals, which had either a completely flat surface (L. depressum, S. dura) or a very complicated surface, with numerous ridges or finger like projections (L. venustum, S. leptoclados). In these cases the index would not have made sense and was not used.

Also a meandrization index, as formulated by Veron et al. (1977), was used to describe the degree of fusion of individual corallites into longer series (also referred to as "valleys").

I_m=number of centres/numbers of valleys

The higher the value, the longer the valleys. Monocentric species have an I_m of 1.

Chlorophyll analysis

Chlorophyll was extracted by means of hot methanol extraction (HMSO, 1986) from tissue block of $5mm^3$ taken from different parts of the experimental colonies. Optical densities were read at 664, 647 and 630nm and converted to concentration of total chlorophyll (a, b and c) using the formula derived by Jeffrey & Humphrey (1975).

$$21.78\ (OD_{630})+11.89\ (OD_{647})+4.75\ (OD_{664})=\text{ug chlorophyll}$$

Results

a) Reactions to short-term sedimentation

1) Clearance rates and the influence of colony morphology

It was apparent that major differences existed in the clearance rates and clearing efficiencies of hard and soft corals (Table 1, Figs. 2&3). With the exception of S. glaucum, soft corals were less efficient than hard corals (Fig. 3). Within these two categories differences also existed. The most obvious factor governing the ability of the hard corals to reject sediment was their colony shape. The runoff and spontaneous clearance rates (sediment recovered in the first 10 minutes) were significantly higher in very spherical corals (sphericity index 0.4-0.5) than in flatter specimens (sphericity index less than 0.4, t-test, $t=-4,01$ $p<0.01$). In hemispherical colonies there were significant differences in the clearing rate with time (ANOVA, $F=42.8$, $p<0.001$), clearance being markedly higher in the first ten minutes. Much of this high clearance could be attributed to passive runoff. However, over the entire period, no correlation existed between sphericity and clearance rate and efficiency in hard corals ($R=0.53$, $p>0.05$ with fine sand; $R=0.30$, $p>0.05$ with medium sand; $R=0.37$, $p>0.05$ with coarse sand; Table 1) indicating the importance of other morphological and behavioural factors. No differences in clearing rates with time were observed in flat colonies of sphericity indices less than 0.4 (ANOVA, $F=0.92$, $p>0.05$), indicating a more even rate of sediment rejection. The overall success of sediment rejection was not only due to sphericity, as no significant differences existed in the overall clearance success (over the entire period) between the groups with sphericities less than 0.4 and those with higher sphericities (t=-

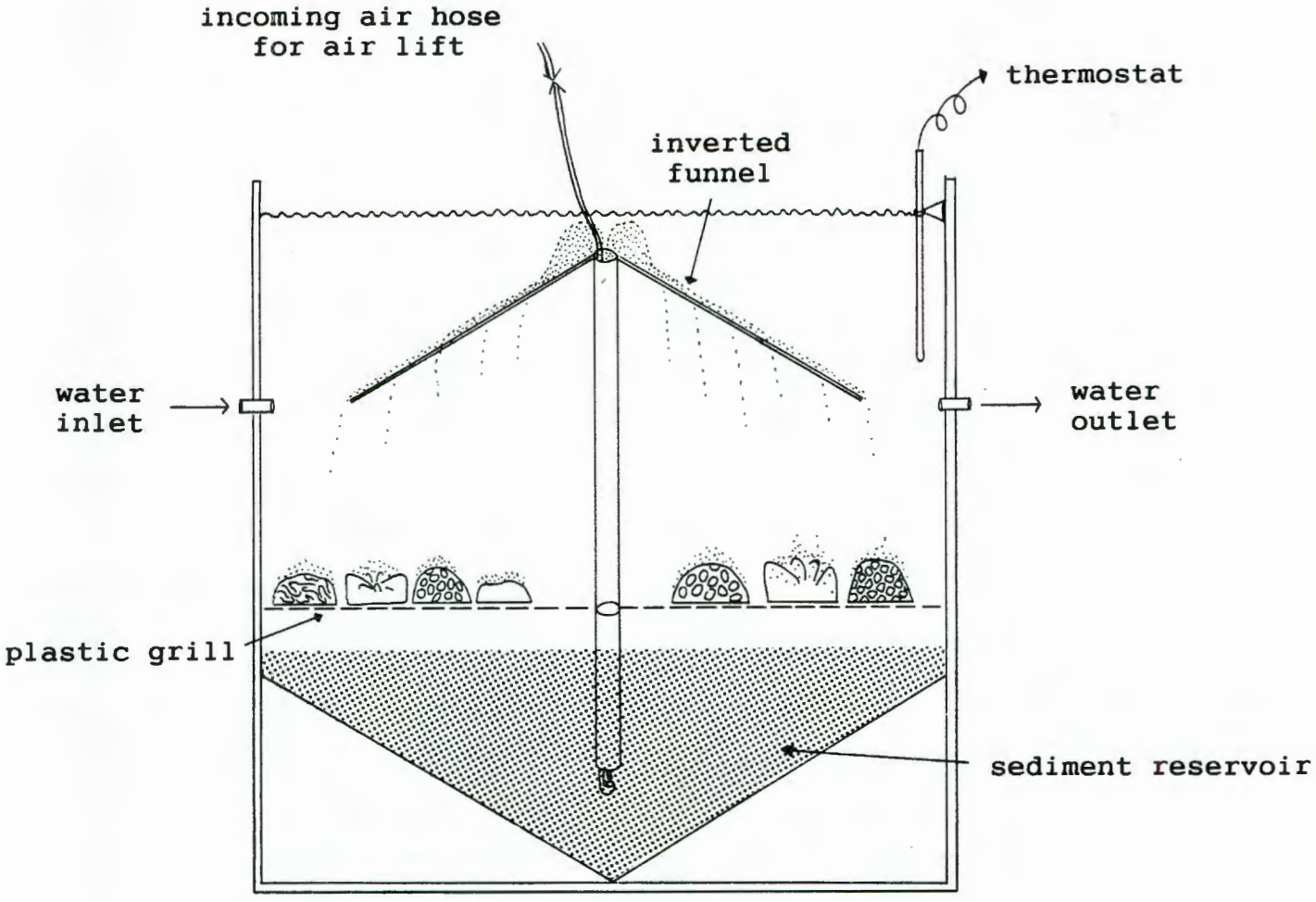


Fig. 1: The apparatus used to create a permanent high sedimentation environment. Experimental corals were placed on a plastic grid, which did not allow any accumulation of sediment other than on the animals themselves. Sediment was sucked up inside the central column by means of an air-lift and distributed evenly over the experimental area with the help of an inverted funnel perforated at regular intervals. A circular current in the basin evenly distributed the sediment. Water supply was flow-through, total water replacement in the aquarium was once every hour.

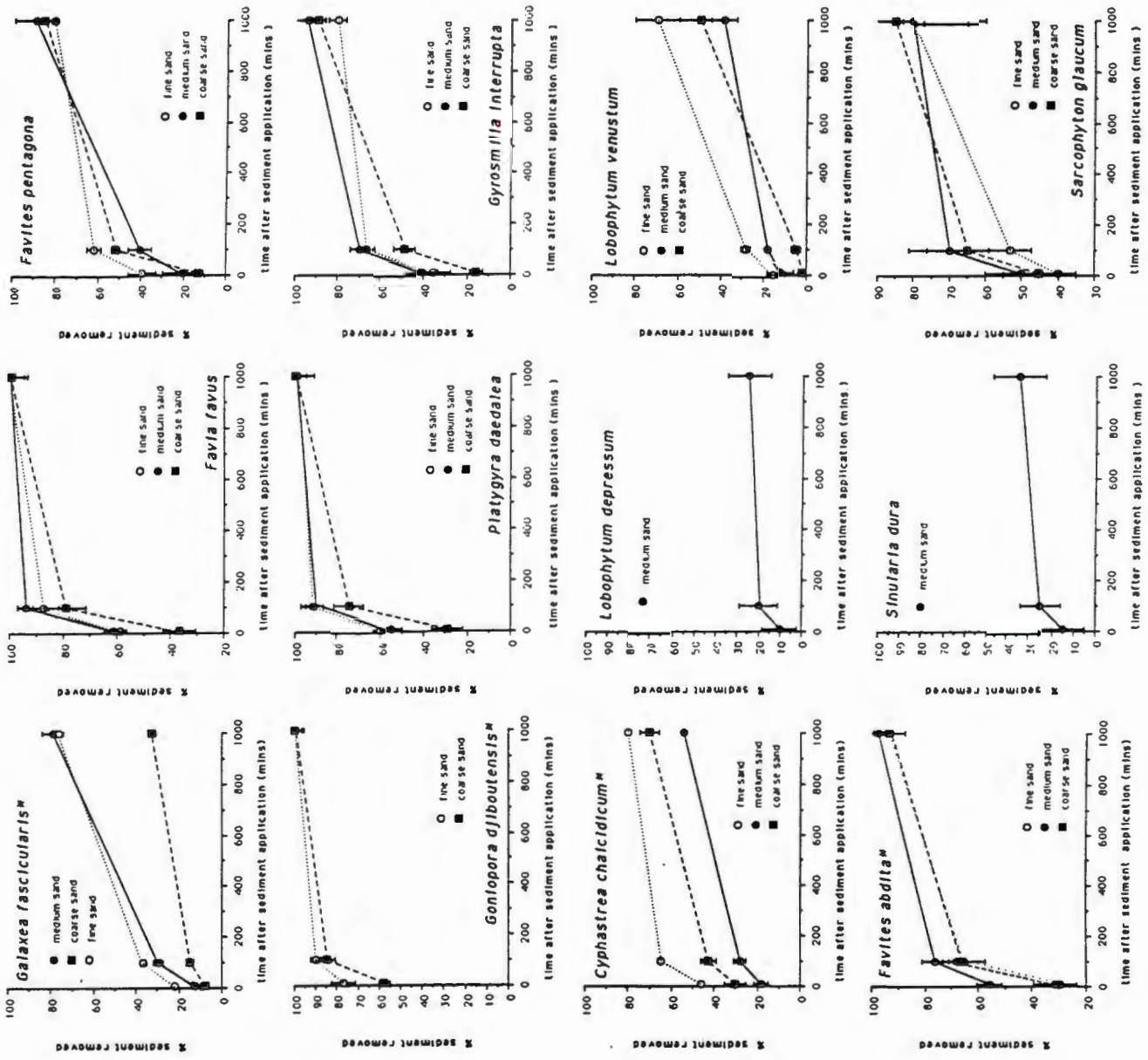


Fig. 2: Cumulative sediment rejection by the tested hard- and soft coral species. Species indicated with an asterix were represented by a single specimen only. All other species were properly replicated. Not all species were tested with all grain sizes, this is indicated in the graphs.

0.56, $p>0.05$ with fine sand; $t=-1.15$, $p>0.05$ with medium sand; $t=-0.03$, $p>0.05$ with coarse sand). All the hard corals succeeded in clearing over 50% of the applied sediment off the corallum within 1000 minutes. Calyx size was an important factor in aiding sediment clearance (Fig. 4a-d), as the species with larger polyps cleared fine sediment faster than the species with smaller polyps: there existed a linear relationship between calyx size and clearance rate in plocoid corals (Galaxea fascicularis, Cyphastrea chalcidicum, Favia favus, Favites pentagona, Goniopora djiboutensis, Hydnophora microconos) with fine sand but not with the other sediment types. A significant correlation was also evident when the data were averaged for all three types of sediment (Fig. 4). No significant correlated existed between the number of calyces per surface area unit and clearance rate, although there was a consistent pattern for the relationship to be negative ($r=-0.44$, $p>0.05$ with fine sand, $r=-0.54$, $p>0.05$ with medium sand; $r=-0.49$, $p>0.05$ with coarse sand). In meandroid species, the degree of meandrization was of importance, as clearance rate increased with increasing meander length, at least in the case of medium sand (Fig. 5a-d). There were no differences in clearing rates between plocoid and meandroid species (Favia favus, Favites pentagona, Cyphastrea chalcidicum, Favites abdita versus Platygyra daedalea, Gyrosmilia interrupta: $t=-2.2$, $p>0.05$ with fine sand; $t=-1.91$, $p>0.05$ with medium sand; $t=-1.89$, $p>0.05$ with coarse sand).

The soft corals showed much less activity in rejecting sediment than the hard corals. The runoff rates were low due to the flat growth forms, except in small specimens of Sarcophyton glaucum (around 5 cm in length), which bent under the weight of the

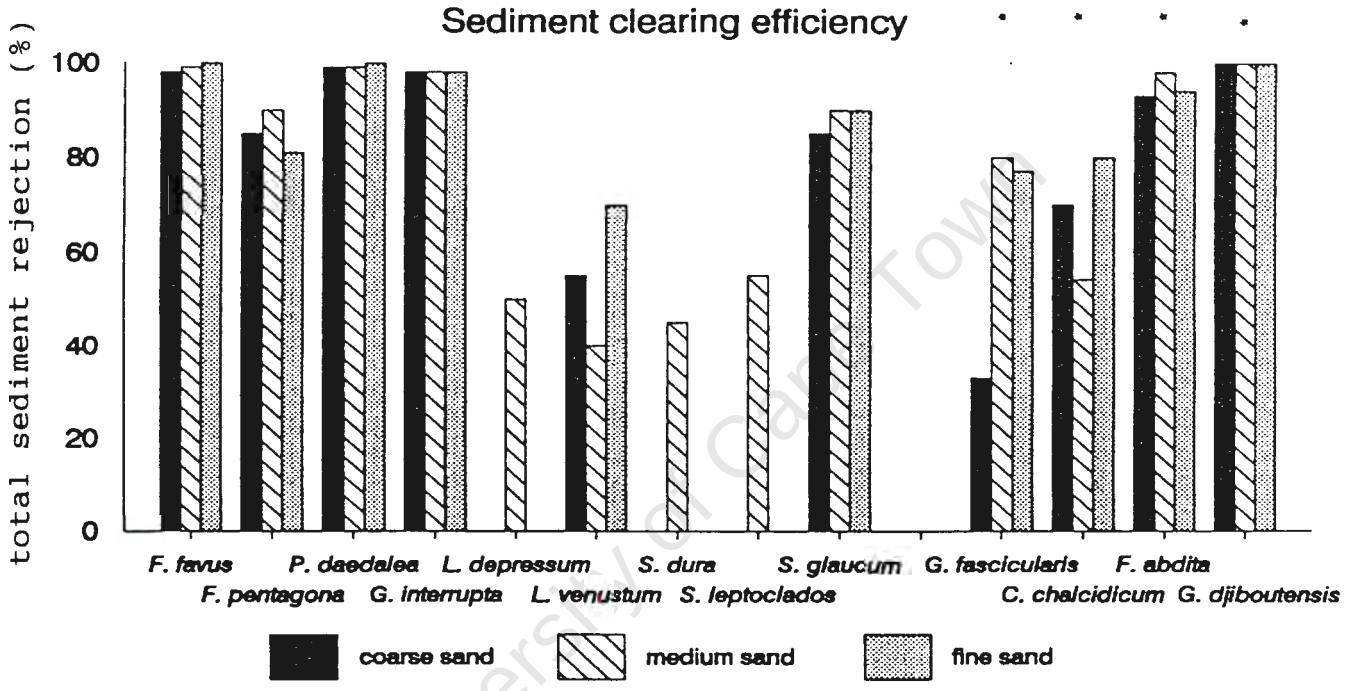


Fig. 3: Sediment shedding efficiency of the experimental species within a 1000 minute period. Values are proportion of applied sediment cleared by the corals. Lobophytum depressum, Sinularia dura and Sinularia leptoclados were only tested with one single grain size sand. Data for species indicated with an asterisk were obtained from a single specimen only.

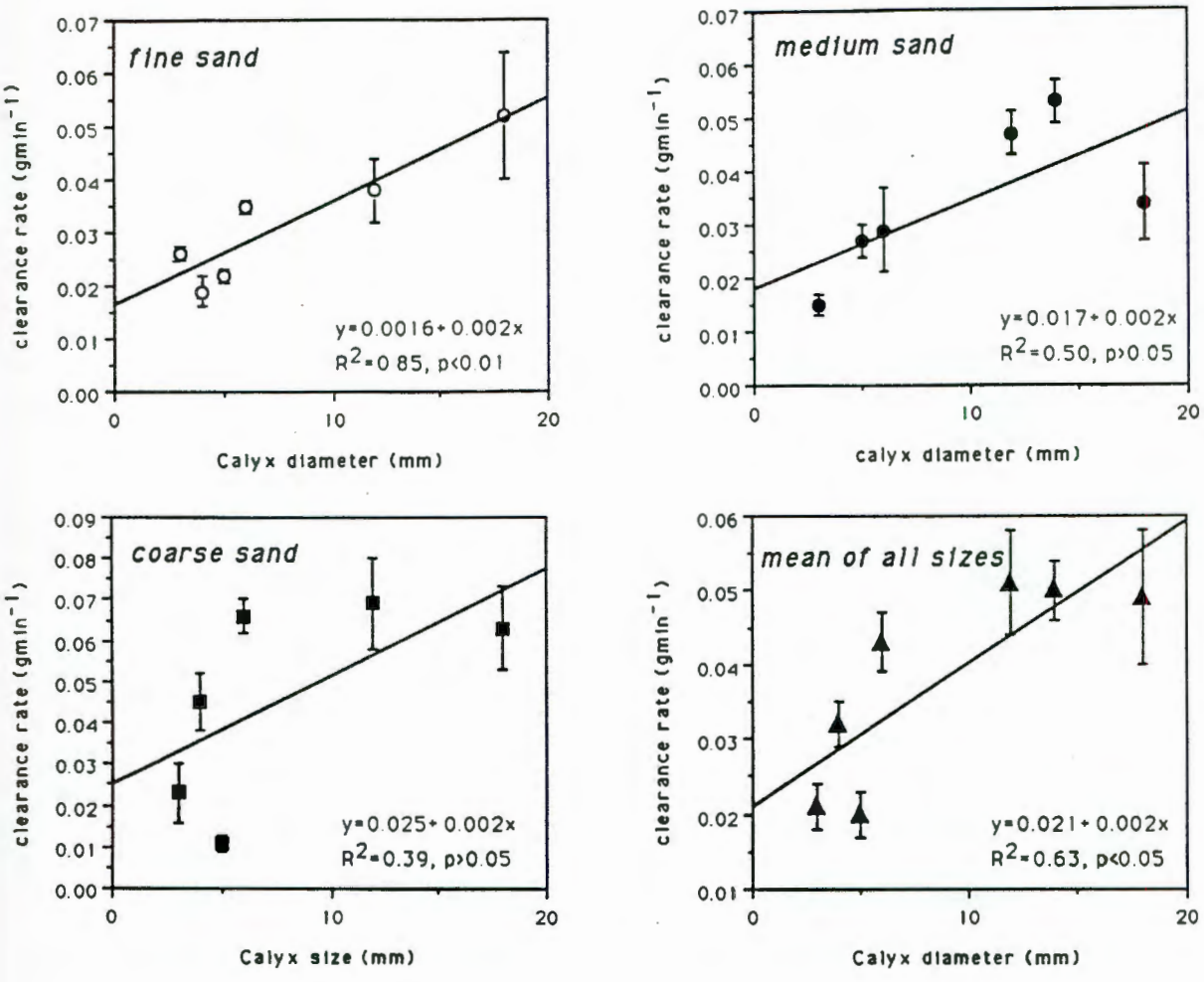


Fig. 4: Relationship between calyx diameter and clearance rate in the plocoid species (see table 1).

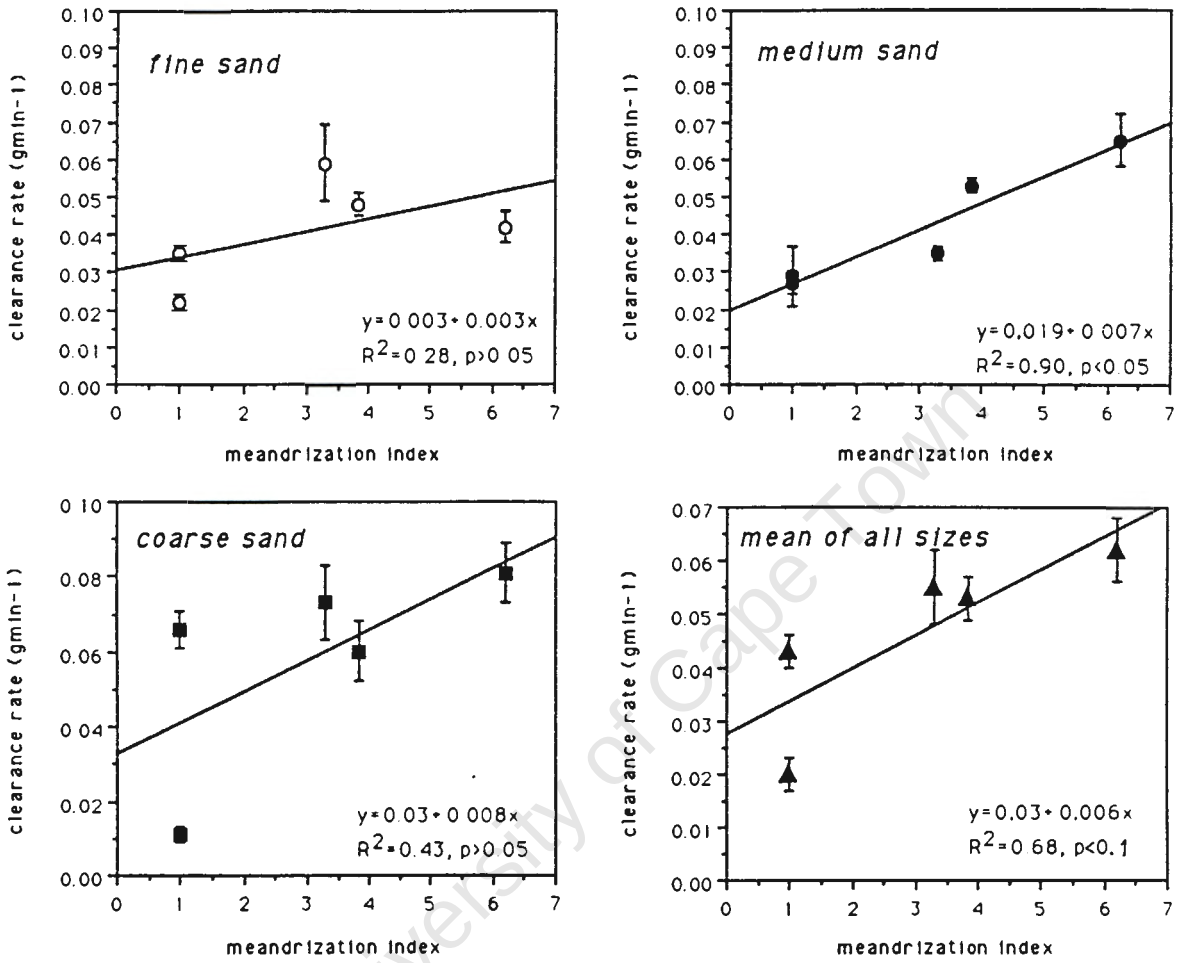


Fig. 5: Relationship between meandrization index and clearance rate in the meandroid species (see table 1).

sediment. This was not the case in a large specimen (20 cm length). However, no active clearing behaviour was observed in this species and in bigger specimens none of the sediment on flat parts was removed. In the other species of soft coral, morphology also played a role in aiding run-off or in concentrating the sediment in certain areas of the colony. Runoff and concentration of sediment in certain areas was enhanced by the radially arranged ridges in Lobophytum venustum and some specimens of Sinularia dura, and the finger-like projections in Sinularia leptoclados. None of the soft corals showed any polyp-activity or other visible reactions to short-term sediment application. Inflation of the colonies by as much as 30% of their resting volume was observed in all species.

In hard corals there were significant differences in sediment clearance success between the time intervals 10, 100 and 1000 minutes (ANOVA, $F=8.026$, $p<0.001$) with most cleared sediment recovered in the first ten minutes (Fig.2). This was entirely due to runoff. Also, in soft corals there were significant differences in sediment clearance between the time intervals ($F=14.07$, $p=0.0008$). Unlike the hard corals, however, most sediment was rejected in the time between 100 and 1000 minutes after application (Fig. 2). This indicated a slower sediment shedding response.

Behavioural response to sedimentation was mainly of two types. The first reaction was hydrostatic inflation of the polyps of the hard corals, or of the entire corallum of the soft corals. This reaction greatly enhanced the runoff, especially from hemispherical hard corals and from the sloping edge of soft coral colonies. Favia favus and Favites pentagona used mainly their

inflated polyps to reject sand. On flat coralla of Favia favus, Favites pentagona, Hydnophora microconos and Platygyra daedalea, differential inflation of polyps in specific areas was used to shift the sediment. Removal of sediment led to eventual deflation (within 30 minutes) of the polyps. Disposal of sediment by tentacular action was observed in Gyrosmilia interrupta. Platygyra daedalea used inflated polyps, ciliary activity was inferred, but could not be proven, by the way this species moved sediment along the valleys of fused corallites. It is likely that cilia on the oral field helped move the sediment concentrated in certain areas by the inflated polyps.

2) Effect of different grain sizes

There were no significant differences in clearance efficiency after 10, 100 and 1000 minutes, overall clearance efficiency and calculated clearance rates between the three types of sediment used (ANOVAs, $F=2.554$, $p=0.09$ in the first ten minutes; $F=0.773$, $p=0.47$ after 100 minutes; $F=0.125$, $p=0.883$ after 1000 minutes; $F=1.19$, $p=0.32$ for clearance rate, $F=0.373$, $p=0.694$ for overall clearing efficiency).

B) Reactions to long-term sedimentation

1) Levels of activity

In hard corals reactions were varied. In Favia favus, Favites pentagona and Platygyra daedalea, first contact with the sediment lead to immediate inflation of polyps. Continued cover by sediment resulted in the extrusion of mesenterial filaments. After a week of continuous sediment coverage many of the polyps were fully stretched and had also extended and inflated their peristome. This

Responses of hard-corals to long-term sedimentation

	F. favus	*F. pentagona*	*P. daedalea*	*G. interrupta*
hydrostat. inflat.	yes	yes	yes	no
tentacular activity	no	no	no	no
increased mucus p.	yes	yes	yes	yes
congealed sediment	yes	yes	yes	yes
small necroses	yes	yes	yes	yes
large necroses	no	yes	no	no
death of colonies	no	no	no	no
local bleaching	no	yes	no	no

Table 2: Responses of hard corals to long-term sedimentation during a 6-week experimental period. Only responses which were observed for more than at least one week at a time are noted.

behaviour continued through the entire experimental period. Gyrosmilia interrupta reacted to the ongoing sedimentation by contracting the previously extended tentacles. During short term sedimentation the tentacles were active in removing sediment, but this behaviour ceased under the long-term sediment stress. These, and other, reactions of hard corals are summarized in Table 2.

All soft corals, except Lobophytum depressum, immediatedly ceased activity with the onset of sedimentation and retracted all polyps. No tentacular activity was discernible. However, similar to the short-term sedimentation experiments, most colonies inflated at the beginning of the experiment. Specimens which suffered tissue damage remained constantly inflated, while the other specimens showed no consistent pattern. Maximum inflation lead to about 30% size increase compared to control conditions. Some Sarcophyton glaucum colonies became limp and deflated at times. This aided clearance of the sediment as it would simply slide off the hood. These specimens also showed inflation of the entire corallum alternating with deflation. The behavioural reactions of soft corals are summarized in Table 3.

2) Tissue necroses

In the hard corals, tissue necroses started to appear after 15 days. In Favia favus, Favites pentagona and Platygyra daedalea necroses formed predominantly on the periphery of the colony. In Gyrosmilia interrupta they formed in the centre of the colony. Over the next two weeks no dramatic changes happened. In one specimen of Favia favus the tissue necrosis healed. In the other specimens tissue necroses, where present, slowly proceeded to approximately double their size. Tissues appeared to be very thin

Responses of soft corals to long-term sedimentation

	L. depressum	*L. venustum*	*S. dura*	*S. leptoclados*	*Sarco. glaucum*
hydrost. inflation	yes	yes	yes	yes	no
polyps expanded	partly	partly	no	no	partly
increased mucus p.	yes	yes	yes	yes	yes
congealed sedim.	yes	yes	yes	yes	no
small necroses	yes	yes	yes	yes	yes
large necroses	yes	no	no	no	yes
death of colonies	yes	no	no	no	yes
local bleaching	no	yes	yes	yes	no

Table 3: Responses of soft corals to long-term sedimentation during a 6-week experimental period. Only responses which were observed for more than at least one week at a time are noted.

Weight loss in soft corals during the experiment

	% of original weight control	standard error control	% of original weight sedimented	standard error sedimented
L. depressum	75.6	0.6	38.2	22.1
L. venustum	100.0	0.0	74.3	9.2
S. dura	94.0	3.0	85.0	2.3
S. leptoclados	100.0	0.0	69.5	3.8
S. glaucum	75.6	12.1	22.5	22.5

Table 4: Comparison of weight loss of the experimental and control corals over the six week experimental period. Values are the percentage of the original weight at the start of the experiment.

and the early necroses most frequently started to appear on the tops of the thecae in all species. At the end of the experiment (after 4 weeks) most tissue necroses in all hard corals were stable and had not expanded in the last week of the experiment. Only one specimen of Favites pentagona had lost a substantial amount (2/3) of its tissues. In all other specimens and the other species only individual polyps or series of up to three polyps were lost. The reactions of hard corals to long-term sedimentation are summarized in Table 2

Among the soft corals tissue necroses were present in Lobophytum depressum prior to the experiment, and increased in size within three days of the beginning of the experiment. New tissue necroses formed on one specimen of L. venustum and S. leptoclados. In Sarcophyton glaucum, tissue necroses appeared on the hood and the stem. This trend was maintained through the entire course of the experiment. After 14 days one specimen of S. glaucum and 1 specimen of L. depressum died, while no such mortality was observed in the other soft or hard coral species. Tissue necroses continued to be formed and to enlarge in all soft coral species. They were mostly round and formed neat pits, which kept enlarging towards the periphery. Most necroses were located in flat parts of the animals. The most serious necroses were found on S. glaucum and L. depressum. However, while S.glaucum tended to die very quickly ofter the onset of necroses, L. depressum continued to live, despite serious tissue damage. The reactions of soft corals to long-term sedimentation are summarized in Table 3. Soft corals lost significantly more weight in sedimented conditions than in control conditions (U-test, $z=2.2$, $p<0.05$, Table 4). The weight

Effects of local bleaching on
Chlorophyll content

	bleached area	unbleached area	t-value	significance
L. depressum	-	3.13±1.03	-	-
L. venustum	1.41±0.81	3.21±0.63	-4.64	0.0001
S. dura	0.44±0.22	1.06±0.17	-5.36	0.001
S. leptoclados	0.79±0.35	1.71±1.01	-1.711	0.13

Table 5: Chlorophyll content in partially bleached soft corals. Values are in µg Chlorophyll per $5mm^3$ surface tissue. Lobophytum venustum was included for comparative reasons. Sarcophyton glaucum did not bleach.

changes in hard corals were not high enough to be detectable against the background of the heavy skeleton.

3) Bleaching

Serious bleaching was observed after 5 weeks on the soft corals Lobophytum venustum and Sinularia dura. Only the central, flat part of the colony was concerned, the ridges, which at no stage were completely covered by sediment, did not bleach. Significant differences were found in the chlorophyll concentrations of bleached and non-bleached parts in two of the three species (Table 5). Of the hard corals, only one specimen of Favites pentagona bleached shortly after the beginning of the experiment.

4) Mucous sheets

No mucous sheets comparable to those observed under natural conditions were observed during the entire experiment. However, in all soft corals of the genera Lobophytum and Sinularia sediment particles were stuck to the surface of the colonies by what seemed to be congealed mucus. In hard corals the presence of mucus was inferred by sediment particles being stuck together and hanging from the edge of the colonies. This was most frequently observed in the flat specimens. The formation of mucous sheets did not occur in the hard corals either.

Discussion

The results of this study show clearly, that while all tested hard and soft corals are very well able to withstand short-term sedimentation, long-term sedimentation results in various stress responses or death of entire colonies. It has also become obvious

that colony morphology plays a crucial part in the coral's ability to cope with short- and long-term sedimentation. In hard corals the sphericity of colonies is of importance in the early phases of sediment shedding, influencing the relative ability of a colony to clear sediment quickly. The flat specimens always fared worse than the hemispherical ones, especially in the long-term sedimentation experiment. While in very rounded specimens tissue death was restricted to peripheral areas, where the shed sand accumulated, flat specimens also suffered severe tissue necroses in the central part of the colony.

This study showed that in some cases calyx size influenced the rate or efficiency of sediment clearance. Although it seems to be a generally observed phenomenon (Hubbard & Pocock, 1972; Hubbard, 1973; Stafford-Smith, 1993), it is not fully clear why calyx size should have a strong influence on sediment clearance. The general behavioural response of most hard corals to sedimentation seems to be polyp inflation (Stafford-Smith, 1993; this study), the inflated polyps then form a smooth surface from which sand can run off easily, so I see no intrinsic advantage for sediment shedding in having larger polyps. In this respect it is also not surprising that no differences existed in the sediment clearing efficiency of meandroid and plocoid corals. However, both meandroid species (P. daedalea and G. interrupta) were not able to inflate their polyps to a similar extent as the plocoid species (Favia favus and Favites pentagona), which may indicate that other mechanisms like increased ciliary activity (as suspected for Platygyra daedalea) or tentacular action (as observed in Gyrosmilia interrupta) play an important role. It is however interesting to note, that within meandroid species the specimens with longer valleys tended to have

a faster sediment clearance rate, although no statistical relationship existed apart from the case of medium sand. This may indicate that the valleys serve as canals for the transportation of sediment and that longer valleys fulfil this function better due to the absence of obstacles in the path of the sediment being removed.

The morphology of soft corals seemed to ensure that at least some parts of the colony were not covered by sediment. The numerous radial ridges in L. venustum and S. dura, as well as the finger-like projections in S. leptoclados always kept a large portion of the corals' surface above the sediment. The parts which were covered, however, did suffer, especially under permanent sedimentation, as can be seen from the formation of tissue necroses and localized bleaching.

The behavioural responses of corals to short-term sedimentation seemed always to be of a nature which would incur the least expenditure of energy. In the short-term sedimentation experiment none of the species changed its behavioural pattern after the application of sediment. In species in which the polyps were extended before sediment loading (G. interrupta, Goniopora djiboutensis), retraction was only observed immediately after the impact of the sediment. Shortly afterwards the corals began with cleaning activity using their tentacles. In hard corals where the polyps were retracted before sediment loading, the most common reaction was hydrostatic inflation of the polyps (F. favus, F. pentagona, P. daedalea, F. abdita). Soft corals also inflated, but this alone did not lead to a cleaning effect that was as effective as that in the hard corals. The soft corals appeared to need some external factor like water-motion to help clean them.

Behavioural responses to sedimentation changed only partly in the long-term experiment. Two of the hard coral species (F.favus, F.pentagona) extruded mesenterial filaments in a reaction to long-term cover by sediment. This is normally an aggressive or defensive reaction to other species (Lang & Chornesky, 1990), which probably indicates severe stress of the sedimented animal. The same response was reported by Stafford-Smith and Ormond (1992), but no details are given for what period of time sediment was applied. It appears however, that they observed extrusion of mesentaries as a response to short-term sediment application.

The soft corals did not react differently in any way under long-term sedimentation compared with short-term sedimentation, but many stayed permanantly inflated. Inflating the corallum or the polyps may also have metabolic advantages, apart from only forming a rounder shape which promotes run-off. As a layer of sediment might hinder nutrients or waste from reaching or leaving the coral by means of diffusion, a greater amount of water circulating within the coral might compensate for the loss of active outer surface area.

Increased mucus production was indicated by a thick mucous layer enveloping numerous sand grains, which thus stuck to the coral's surface. However the production of mucous sheets (Coffroth, 1988) was not observed in the laboratory, only in the field.

In the long-term sedimentation experiment it appeared that the corals' efforts to clear themselves of persistant sedimentation changed from a minimal response, like polyp inflation, to energetically more expensive responses, such as increased mucus production. As the experiment continued, the reactions of the corals and their cleaning attempts eventually faded. It appeared

that most corals were exhausted after about a week of continuous sedimentation and shortly afterwards serious tissue necroses started developing. Physiological implications of this observation were examined in detail in the preceeding chapter.

As the dominant reaction of all corals to sedimentation was to promote runoff rather than active transport of particles, it is not surprising that differnt grain-sizes in the experimental sand did not have any effects on the clearing reactions, clearing speeds and clearing efficiencies of the corals.

The reactions of the tested hard and soft corals also allowed conclusions to be drawn about processes underlying coral community structure on South African coral reefs. I have speculated in a previous section of the thesis (Part II), that soft corals only dominate in areas of lower sedimentation, such as reef tops, while high sedimentation environments, such as gullies, are characterized by hard corals. The results of the present study support these assumptions. As no behavioural reaction towards the clearing of accumulated sediment was observed in any of the soft coral species, it is assumed that these animals rely on water motion to keep them clean. Sediment may be washed off or, if mucous sheets (Coffroth, 1988) have been formed, the entire mucous sheet plus sediment may be removed by water movement, leaving the animal clean. This mechanism would explain why most soft corals, and particularly Lobophytum venustum and Sinularia leptoclados are found in elevated parts of the reefs at Sodwana Bay, where sediment deposition is low and water motion high in times of heavy surge. The two species of soft coral which occur within gullies and higher sedimented areas on Sodwana reefs, Lobophytum depressum and Sinularia dura, showed no obviously different reactions to

applied sediment when compared with the other soft corals. They do not seem to be adapted to a high-sedimentation environment. Most colonies were found growing on the near vertical gully walls. The orientation of such colonies then makes it impossible for sand to accumulate on them. Sarcophyton glaucum, while suffering heavy losses when subjected to permanent sedimentation, appeared to cope quite well with short-term application of sediment. Its growth form allowed the colony to bend and shed most of the sediment. This may allow this species to persist in areas with temporarily elevated levels of sedimentation.

Hard corals, on the other hand, were very active in shedding and promoting run-off of accumulated sediment and die-back and bleaching levels were much lower than in the soft corals. It is therefore assumed that they are better adapted to an environment with higher sedimentation, which would explain why they are equally common inside and outside gullies on South African reefs. Due to the relative scarcity of soft corals in these environments hard corals dominate areas of higher sedimentation on these reefs. This study therefore supports the conclusion that sedimentation is a major forcing factor influencing the structure of South African coral communities.

Conclusion

Differences exist in the reactions of hard and soft corals to short-term and long-term, artificially induced, sedimentation. The basic reaction to sedimentation was the same in hard and soft corals, namely hydrostatic inflation of the polyps (in hard corals) or the entire colony (in soft corals). Due to their shape and bigger polyps, hard corals were, however, much more efficient

sediment shedders. Morphology was very important in the corals' ability to shed sediment and influenced the rate of shedding. In hard corals the most advantageous colony form was hemispherical, which allowed a maximum run-off of sediment and greatly facilitated active clearing. Soft corals concentrated sediment on flat parts of the colony, leaving ridges and finger-like projections free. Long-term sedimentation lead to increased behavioral reaction for about a week, after which it stopped, apparently due to energetic exhaustion. After two weeks, tissue necroses started to form; after four weeks partial bleaching was observed in soft corals. Die-back and bleaching was more obvious in soft corals than in hard corals.

Literature cited:

Abdel-Salam, H.A. & J.W. Porter. 1988. Physiological effects of sediment rejection on photosynthesis and respiration in three Caribbean reef corals. Proc. 6th Int. Coral Reef. Symp., Australia, Vol. 2: 285-292.

Bak, R.P.M. & J.H.B.W. Elgershuizen. 1976. Patterns of oil-sediment rejection in corals. Mar.Biol. 37: 105-113.

Coffroth, M.A. 1988. The function and fate of mucous sheets produced by reef coelenterates. Proc. 6th Int. Coral Reef Symp., Australia, Vol. 2: 15-19.

Dai, C.F., 1991. Distribution and adaptive strategies of alcyonacean corals in Nanwan Bay, Taiwan. Hydrobiologia 216/217: 241-246.

Dallmeyer, D.G., J.W. Porter & G.J. Smith. 1982. Effects of particulate peat on the behaviour and physiology of the

Jamaican reef building coral Montastrea annularis. Mar.Biol. 68: 229-233.

Dinesen, Z.D. 1983. Patterns in the distribution of soft corals accross the Great Barrier Reef. Coral Reefs 1: 229-236.

Edmunds, P.J. & P.S. Davies. 1989. An energy budget for Porites porites (Scleractinia) growing in a stressed environment. Coral Reefs 8: 37-43.

HMSO, 1986. The determination of chlorophyll a in aquatic environments, vol. 4. in: Methods for the examination of water and associated materials, section 2, London: HMSO.

Hubbard, D.K. 1986. Sedimentation as a control of reef development: St. Croix, U.S.V.I. Coral Reefs 5: 117-125.

Hubbard, D.K. & D. Scaturo. 1985. Growth rates of seven species of scleractinian corals from Cane Bay and Salt River, St. Croix, U.S.V.I. Bull.mar.Sci. 36: 325-338.

Hubbard, J.A.E.B. & Y.K. Pocock. 1972. Sediment rejection by recent scleractinian corals: a key to palaeo-environmental reconstruction. Geol. Rdsch. 61: 598-626.

Hubbard, J.A.E.B. 1973. Sediment-shifting experiments: a guide to functional behaviour in colonial corals. in: Boardman, R.S., A.H. Cheethan, A.G. Coates, W.A. Oliver & F.M. Bayer (eds.): Animal colonies. Stroudsburg: Dowden, Hutchinson & Ross: 31-42

Jeffrey, S.W. & G.F. Humphrey (1975). New spectrophotometric equations for determining chlorophylls a, b, c_1 and c_2 inhigher plants, algae and natural phytoplankton. Biochem. Physiol. Pflanzen 167: 191-194.

Lang, J.C. & E.A. Chornesky. 1991. Competition between scleractinian reef corals - a review of mechanisms and

effects. in: Dubinsky, Z. (ed.): Coral Reefs - Ecosytems of the world 25; Elsevier, Amsterdam: 209-252.

Lasker, H.R. 1980. Sediment rejection by reef corals: the roles of behavior and morphology in Montastrea cavernosa (Linnaeus). J.exp.mar.Biol.Ecol. 47: 77-87.

Peters, E.C. & M.E.Q. Pilson. 1985. A comparative study of the effects of sedimentation on symbiotic and asymbiotic colonies of the coral Astrangia danae Milne Edwards & Haime, 1849. J.exp.mar.Biol.Ecol. 92: 215-230.

Rogers, C.S., H.C. Fitz, M. Gilnack, J. Beets & J. Hardin. 1984. Scleractinian coral recruitment patterns at Salt River submarine canyon, St. Croix, U.S.V.I. Coral Reefs 3: 69-76.

Rogers, C.S. 1990. Responses of coral reefs and reef organisms to sedimentation. Mar.Ecol.Progr.Ser. 62: 185-202.

Stafford-Smith, M.G. & R.F.G. Ormond. 1992. Sediment-rejection mechanisms of 42 species of Australian scleractinian corals. Aust.J.Mar.Freshwater Res. 43: 683-705.

Stafford-Smith, M.G. 1993. Sediment-rejection efficiency of 22 species of Australian scleractinian corals. Mar.Biol. 11: 229-243.

Tomascik T. & F. Sander, 1987. Effects of eutrophication on reef-building corals. III. Reproduction of the reef building coral Porites porites. Mar.Biol. 94: 77-94.

Veron, J.E.N., M. Pichon & M. Wijsman-Best. 1977. Scleractinia of Eastern Australia. Part 2, Families Faviidae, Trachyphylliidae. Austral. Inst. Mar. Sci. Monogr. Ser. 3': 1-233.

Wittenberg, M. & W. Hunte. 1992. Effects of eutrophication and sedimentation on juvenile corals. I. Abundance, mortality and community structure. Mar.Biol. 112: 131-138.

P A R T IV

The practical use of it all: Using ecological information to help conservation of the studied ecosystem

In this fourth and final part of my thesis I use the information gathered in all previous parts to suggest new management options to the Natal Parks Board, the conservation authority in charge of the studied coral communities.

MANAGEMENT OPTIONS FOR THE ST. LUCIA AND MAPUTALAND MARINE RESERVES (N-NATAL, SOUTH AFRICA)

Abstract

The information gathered in the previous chapters about ecological patterns and processes underlying the coral communities in northern Natal is used to provide management options for the marine reserves within which these communities are situated. Three basic community types were identified using a structural typology approach. It is suggested that use of the reefs should be limited according to the sensitivity of their communities to damage by human activities. Therefore it is suggested to limit access to 4-Mile Reef in the Central Reef Complex, while no restrictions need to be imposed on the other reefs. Due to the prevailing currents it is suggested that a sanctuary area be enforced in the Northern Reef Complex rather than in the Southern Reef Complex. Reefs in the Northern Reef Complex are more diverse and could serve as larval reservoir for restocking the downstream reefs. The general condition of northern Natal reefs with respect to damage by divers, oil pollution, general pollution, crown of thorns etc. is discussed. No degradation of the reefs was observed.

Introduction

The previous chapters have given us insight into the hermatypic hard-coral fauna of South Africa, the coral community structure on the various reefs and the major forcing factors on these communities. As these reefs are situated within the boundaries of two marine reserves (the St.Lucia-North and Maputaland Marine Reserves), it is possible to use the now available information about pattern and processes within the coral communities to provide management options based on a sound understanding of the area's ecology. Coral reefs have been identified as systems of particularly high value to conservation (Kenchington, 1988). This is partly due to their biological richness, for coral reefs rank among the world's most diverse ecosystems, but also beccause of their enormous appeal to the tourism industry (Rogers et al, 1988; Sybesma, 1988). South Africa's coral reefs are witnessing ever increasing popularity, with big game fishing, spearfishing, snorkelling and particularly SCUBA-diving being the most commonly practiced recreational sports on the reefs. While all South African coral reefs have been in the custody of the Natal Parks Board and have also been managed by this authority, the question has arisen, whether special management options had to be found. Tourism in areas administered by Conservation Bodies provides welcome revenue which can be reinvested in the continued preservation of the money-producing resource or other systems in need of conservation. It is also necessary for provincial or national conservation bodies to make the areas under their legislation available and beneficial to the general public.

I have therefore attempted to provide management options for the coral reefs within the St.Lucia (North) and the Maputaland Marine

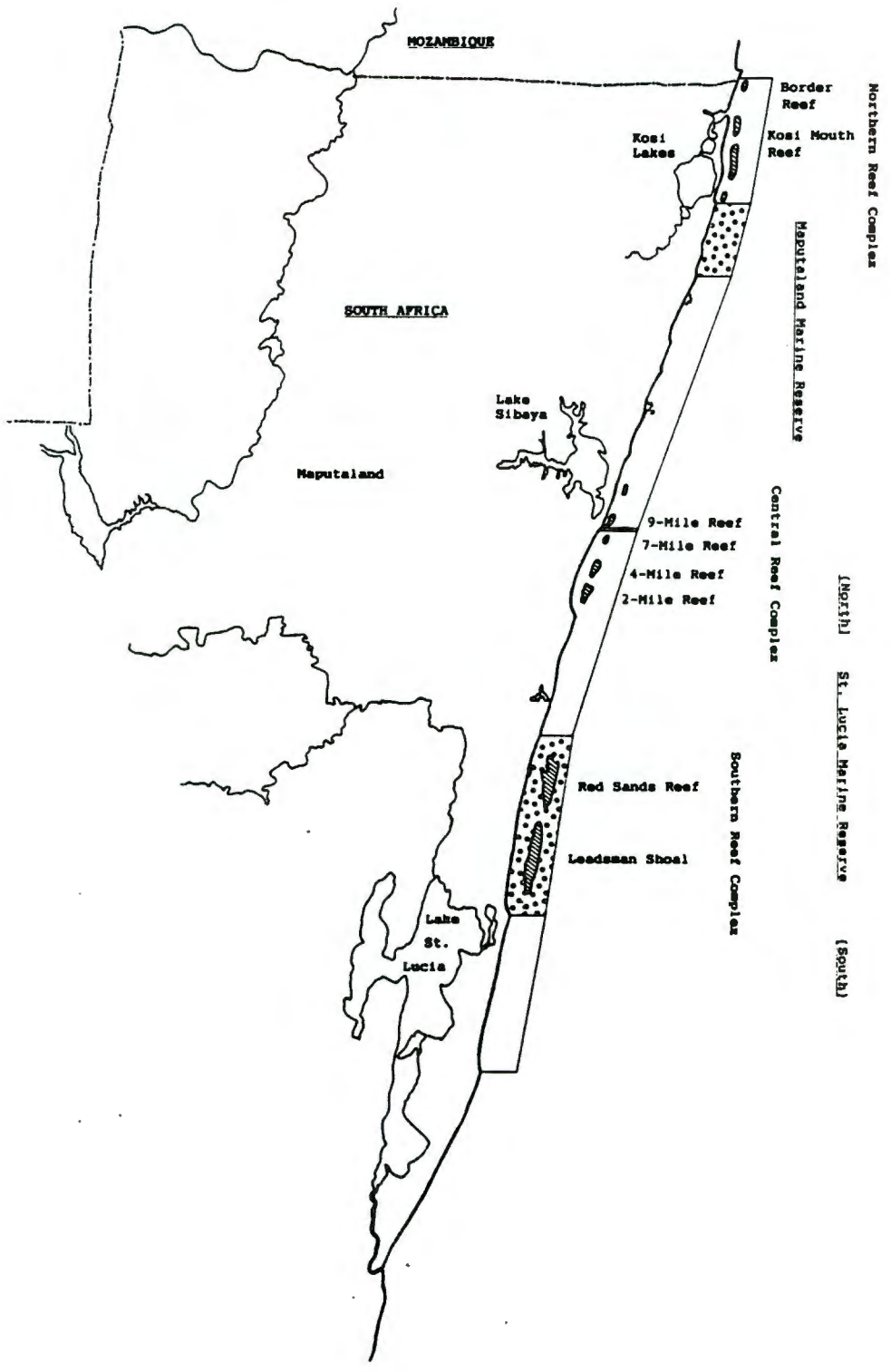


Fig. 1: The location of coral reefs in Maputaland in northern Natal, South Africa. Coral reefs are indicated as shaded areas. The Marine reserves extend from the high-water mark three nautical miles seaward. The two dotted areas (one in the St. Lucia and one in the Maputaland Marine Reserve) are the sanctuary areas, where no human activities are permitted.

Reserves, which will allow a maximum number of visitors to enjoy the reefs while doing the least damage to the coral communities. The management options discussed in this paper are based on studies on the patterns and processes underlying South African coral communities (see previous chapters).

Material and methods

The location of South African coral reefs relative to the marine reserves is indicated in Fig. 1. The biological patterns of coral communities on these reefs are discussed in Part II and the geological setting in Ramsey & Mason (1990). Coral community analysis was performed using the line transect method (Loya, 1978). The transects were then subjected to correspondence analysis (Digby & Kempton, 1984) in order to realize patterns within the communities. All reef complexes were surveyed, although emphasis was laid on studying the Central Reef Complex, which receives most visitor pressure. Having quantitatively surveyed the reefs and determined the coral community types, additional qualitative observations were used in order to provide information on every reef. This was neccessary for drawing up a map of coral community distribution in the Sodwana Bay region.

Quantitative damage assessment was performed using the same modified line transect methods as in Riegl & Velimirov (1991).

Figures of diver-frequency per reef were obtained from the warden in charge of the marine reserves based at Sodwana Bay National Park. These figures were obtained by means of an obligatory questionnaire filled in by each boat operator previous to the launch, indicating the duration and destination of the trip, what activities were going to be pursued and, if diving was going to

take place from the boat, the number of divers and the reef visited. Daily records have been kept since 1986. As all reefs are only accessible by boat, it is thus possible to determine the exact number of dives on each reef and to identify areas of highest pressure.

In an attempt to identify those coral communities most prone to damage by recreational use, I adopted the concept of structural typology, as described by Bradbury et al. (1986) and Bak & Povel (1988), to re-evaluate the coral communities described in Part II. This type of analysis concentrates on describing communities using physical attributes of the corals (growth form and shape) rather than taxonomical attributes (identification to species level). As coral growth form is however generally related to damage-susceptability (Riegl & Velimirov, 1991), this approach allows us to assess the likelihood with which damage may occur within any given community type. Using this approach, coral communities were classified into "damage-susceptibility-categories" using the results from the community study in Part II.

As breakage usually is one of the dominant forms of damage due to recreational use of coral reefs (Rogers et al., 1988; Riegl & Velimirov, 1991) it was possible to estimate the effects of breakage in the dominant branching corals using results from Part III, Chapter 1.

Results and Discussion

a) Characterisation of coral communities

The correspondence analysis grouped the transects along two axes, which were determined largely by the frequency of branching corals, such as Acropora, in the transects. A certain amount of

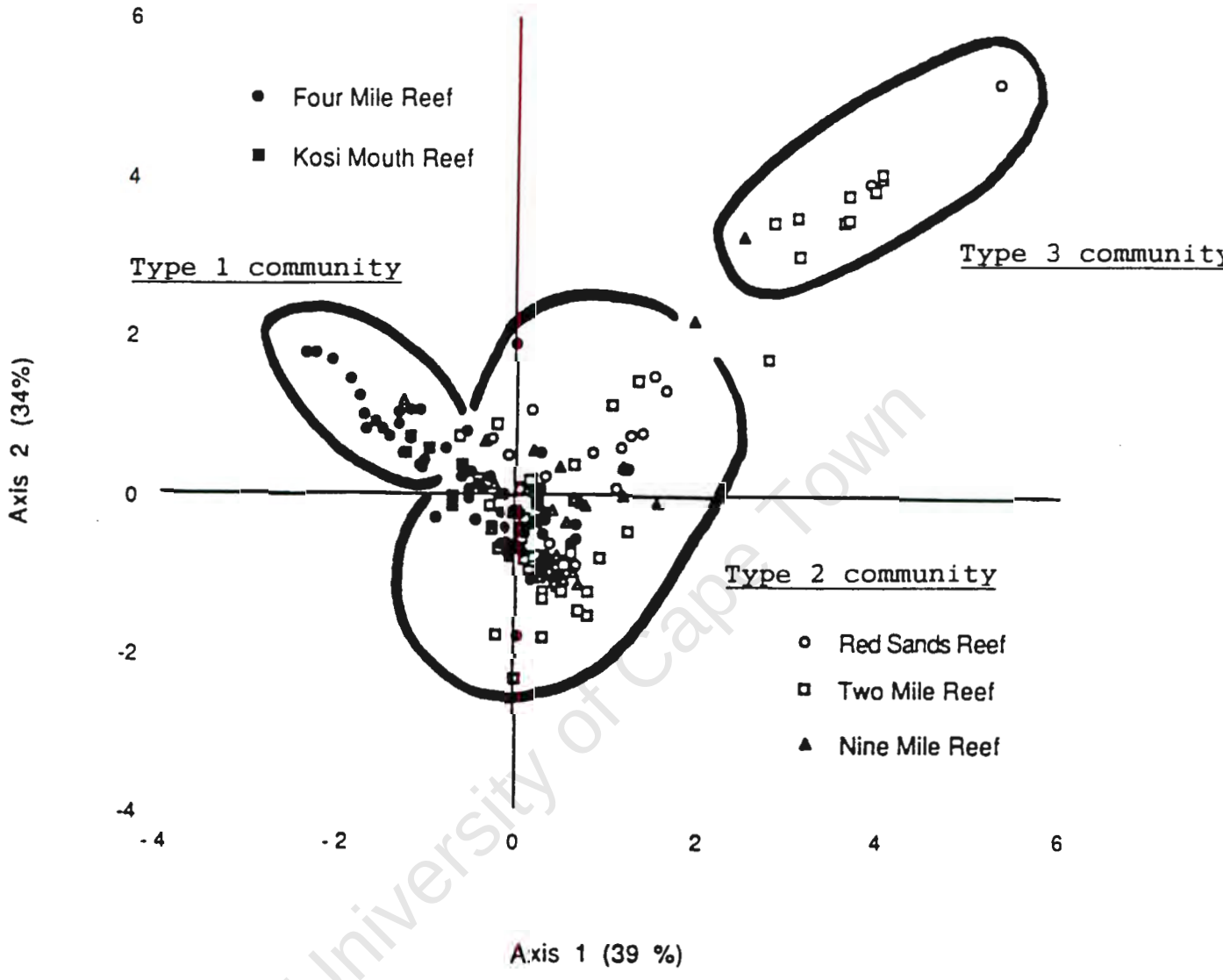


Fig. 2: Ordination by correspondence analysis of all transects obtained from 5 reef sites in northern Natal. Three distinct clusters correlate to three distinct communities characterized by their structural typology.

overlap existed between the clusters, but it was nevertheless possible to correlate the clusters to three distinct coral communities. One cluster, stretching along the negative x-axis, comprised only transects from 4-Mile Reef and Kosi-Mouth Reef, while the second cluster differentiated into two sub-clusters along the positive x- and y-axis. The central cluster, spread around the 0-point comprised transects from almost all sampled reefs; a third cluster, with the greatest distance to all other clusters comprised only transects from greater 25m depth (Fig. 2).

a1) The type 1 coral community

This community is found on the flat, deep outcrops, such as 4-Mile Reef in the Central Reef Complex and Kosi Mouth Reef in the Northern Reef Complex (Fig. 3). It is dominated by hard corals of the genus Acropora. These are either branching A. austera and A. horrida, tabular A. hyacinthus and A latistella or plate-like A. clathrata. All these species are characterized by a greater extension into space than attachment to the substratum. This makes them susceptible to breakage. However, a certain amount of breakage occurs naturally and aids asexual reproduction. Implications of this phenomenon were discussed in Part III, Chapter 1 and will be discussed further in the paragraph on diver interference. Platelike corals, such as A. clathrata, are less in danger of being damaged by divers due to their very thick and robust skeleton.

This type of coral community is particularly sensitive to breakage by careless divers and by anchoring. Repeated anchor drops will reduce even initially large branching or tabular colonies to numerous small fragments with little chances of survival. It has

been shown in other parts of the world that Acropora communities are very susceptible to environmental changes, as could be associated with increased use by tourism, and major losses in Acropora-dominated habitats have been reported (Jaap et al., 1988; Porter & Meier, 1992).

The type I community is the most fragile coral community occurring in South Africa. Measures for its protection should include strict prohibition of anchoring on or near these reefs and a limit to maximum allowable dives per day.

a2) The type 2 coral community

This coral community type is typical of most of the Maputaland Reef Complexes and is the most extensive. It covers most of the hard substrata in less than 18m depth. It is found on all shallow substrata in the Southern Reef Complex (Leadsman Shoal, Red Sands Reef), the Central Reef Complex (2-Mile Reef, 9-Mile Reef) and the Northern Reef Complex (Fig. 3). Within this community type there are further differentiations caused by differential sedimentation levels on the reefs (see Part II). These different subcommunities can however be grouped together for the damage-risk analysis as the growth form of their dominant community members is the same. The typical corals of this community type are soft-corals (genera Lobophytum, Sinularia, Sarcophyton) and massive, hemispherical hard-corals (family Faviidae, Poritidae).

As a consequence, breakage is not a common occurrence and not a natural phenomenon which enhances asexual reproduction in these communities. Any form of coral breakage must be considered as detrimental to the community.

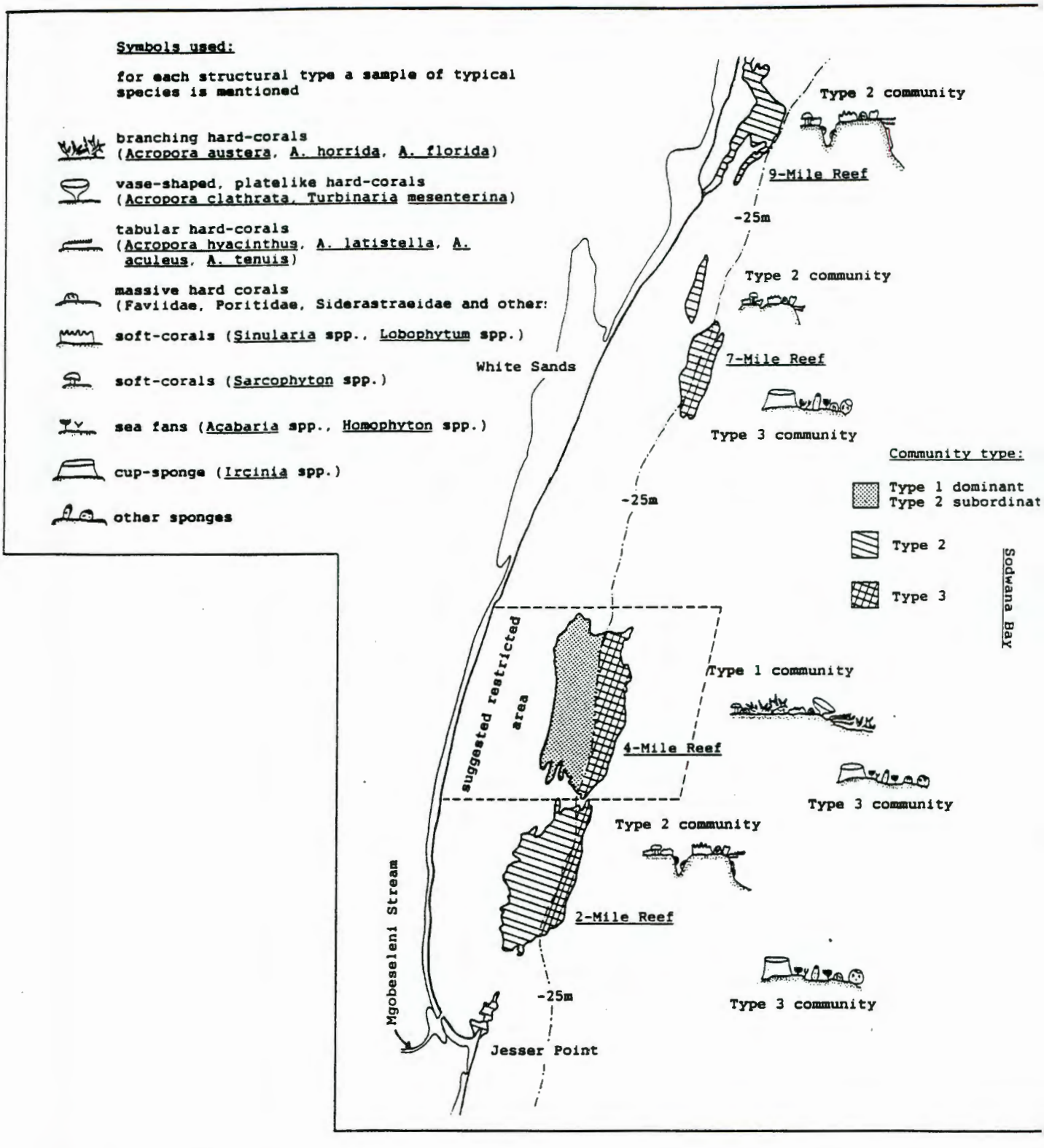


Fig. 3: Distribution of coral reefs and coral community types in the Sodwana Bay area, Central Reef Complex. Map modified after an original by P. Ramsey (1992). The structural typology of the coral communities is indicated by means of symbols explained in a key. Suggested management options, as discussed in the text, are included.

Moreover, the soft-coral dominated "reef-top sub-community" is particularly hardy and tolerant of physical damage, due to the elastic growth form of the soft corals (Wainwright et al., 1976). The major dangers to the corals of these communities are tissue lesions, caused by careless contact with divers, or boat anchors. In the case of hard corals, tissue lesions can become infected by bacteria or algae and lead to outbreakes of diseases like black or white band disease (Antonius, 1985), which can potentially damage large areas of reef. However, none of these diseases have yet been recorded in South Africa. The susceptibility of soft corals to infections has not yet been investigated. A small experiment using the dominant soft coral genera Lobophytum, Sinularia and Sarcophyton, in which $5cm^2$ areas of tissue were cut from 10 colonies each, did not reveal any adverse effects after 3 months. Most corals had already regenerated a third to one half of the lost surface tissue.

a3) The type 3 coral community

This community is only found on the deep parts of the reefs in depths greater than 25m. It occurs on all deep hard bottom areas and has been observed in the Southern Reef Complex (deep Red Sands Reef), the Central Reef Complex (deep 2-Mile Reef ("Sponge Reef"), deep 7-Mile Reef) and the Northern Reef Complex (deep Kosi Mouth Reef, Fig. 3). It is dominated by sponges (cup-sponges, Ircinia spp.) and sea-fans (Acabaria spp., Homophyton spp.). In this area numerous unattached species of hard coral are found (Cycloseris costulata, C. marginata, C. cyclolites, Diaseris distorta), which are easy to collect and may be decimated by poaching. Neither the sponges nor the gorgonians are easily damaged.

As this community grows under very low light conditions at the lower edge of the depth-range of photosynthetic activity in most corals (Part III, Chapter 3), it can be hypothesized, that growth rates may be slow. Damage done to corals at that depth is likely to heal slowly. However, the greater part of the community is made up by sponges and ascidians. In the absence of any data on the susceptibility of these organisms, it is advisable not to allow any activities, which are potentially capable to inflict major damage, like boat anchoring, to take place on these communities. Divers should be strongly discouraged to sit in cup-sponges (Ircinia spp.) or handle any other organisms due to possibly slow regeneration rates.

b) Distribution of diver frequency on the reef

The numbers of divers and dives on northern Natal reefs have steadily increased in the period from 1986 to 1992 (Fig. 4).
From 1990 to 1993, 88% of all dives took place on 2-Mile Reef (Fig. 5). Almost all dives took place in the Central Reef Complex. The distribution of diver frequency on the reefs is such that the highest pressure (i.e. the highest number of divers) is on communities with a low damage-likelihood, as the communities found over most of 2-Mile Reef fall into type two. An increase of diver-pressure on 4-Mile Reef is not desirable, due to the fragility of the coral community. 7-Mile and 9-Mile Reefs are not considered to bear fragile communities and could therfore receive greater numbers of divers.
If restrictions of the number of divers were to be imposed on any reef, this should be done on 4-Mile Reef. The relatively robust communities of all other reefs do not justify such restrictions.

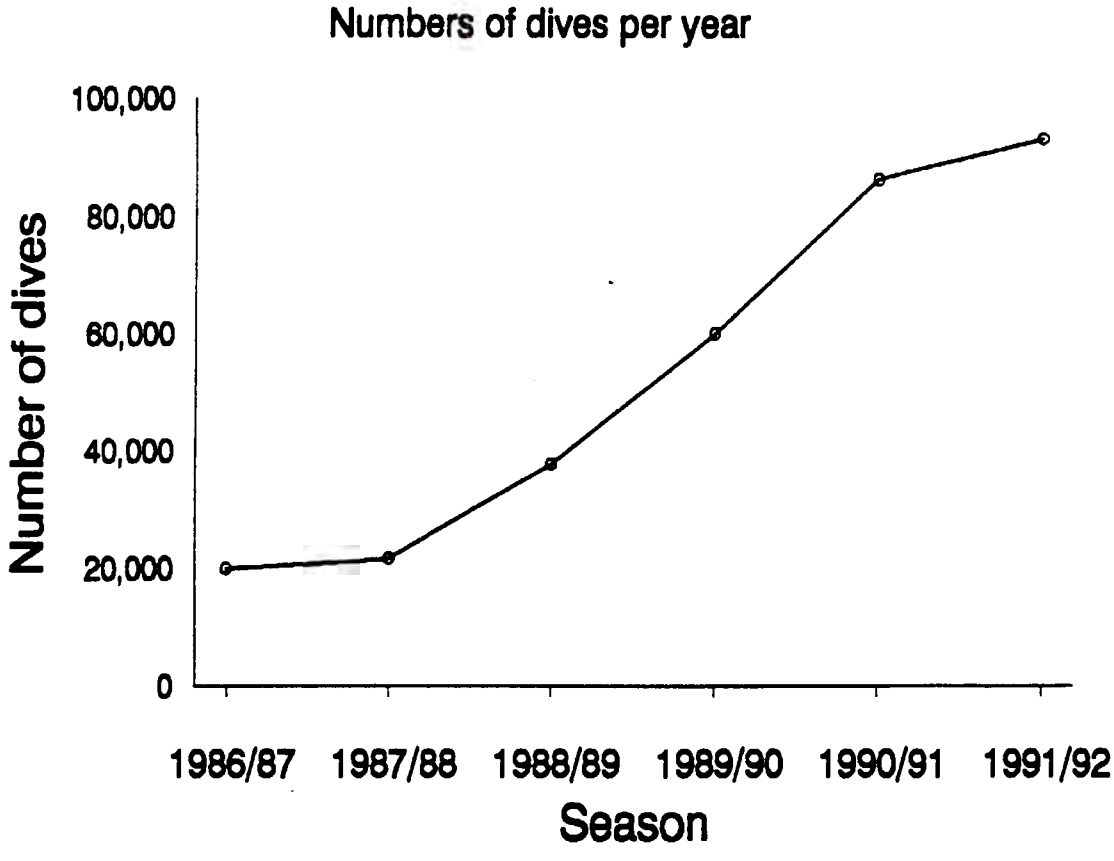


Fig. 4: The number of divers who have been visiting the Central Reef Complex in the Sodwana Bay area as an indication of increased pressure on the reefs.

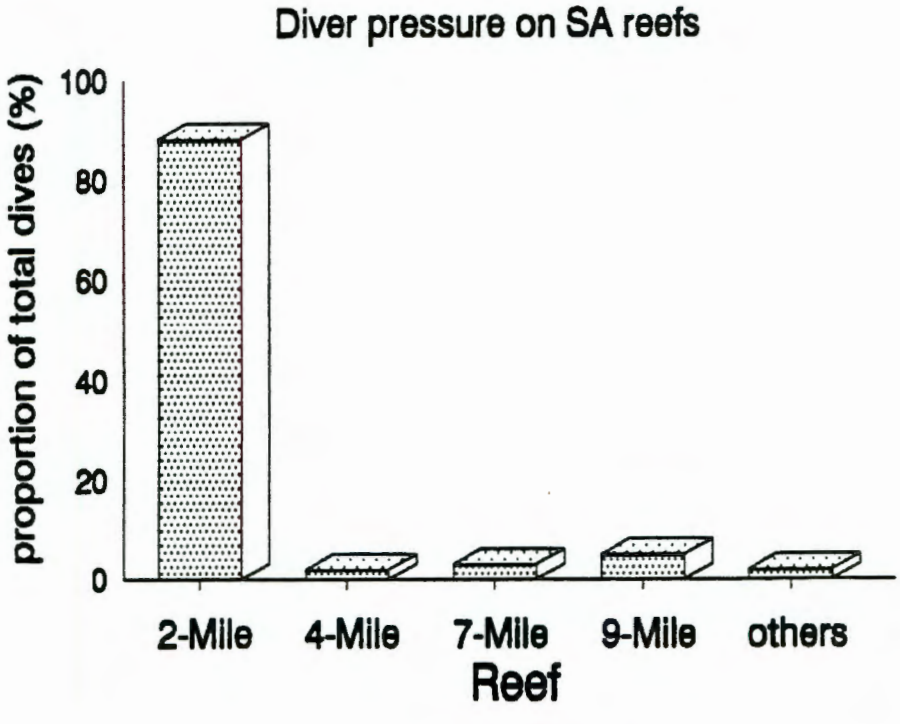


Fig. 5: The distribution of diver pressure on the reefs in the Maputaland and St. Lucia Marine Reserves. Almost all diving takes place in the Central Reef Complex in the Sodwana Bay area.

c) Quantitative damage assessment

Although quantitative damage assessment was undertaken to determine the amount of coral breakage and tissue damage inflicted by reef users, it was discontinued as no sensible results could be obtained. Due to the high wave action on all investigated reefs, broken parts of corals, which are the most common and easily visible signs of diver damage (Rogers et al, 1988; Riegl & Velimirov, 1991), were quickly exported from the reefs. They accumulated in a wide fringe of calcareous fragments around the reefs (Ramsey & Mason, 1990). Due to the short period of time in which the fragments stayed in the area where they were broken, it was not possible to keep track of breakage quantitatively. A general count of all encountered broken fragments was not useful, as it was desired to allocate the fragments to the coral community they were derived from.

While the direct counting approach failed, the nature and species composition of the coral communities made it possible to predict areas susceptible to damage.

d) diver interference

The most common form of diver interference with the coral communities were touching, breakage and resuspension of sediment. Talge (1991) has shown that touching alone has no visible effects on coral health, but speculates that stress may be caused by the removal of mucus via adhesion to the diver's hand (or glove). The possibility that this action might result in stress cannot be excluded. As experiments in Part III Chapter 3 have shown, mucus on the coral surface is very important for the corals and its energetic content is often worth several days of production.

Repeated removal of a large proportion of this mucus could be detrimental to the corals by forcing them to invest energy into regenerating the lost mucus, rather than investing the energy into growth and reproduction.

The effects of breakage on a branching coral (Acropora austera) were investigated in detail in Part III, Chapter 1. The results showed clearly that the mortality of broken parts is very high (only 10% of all fragments survived a three month experimental period). Breakage in shallow areas of the reefs lead to the loss of the fragments and no local regeneration is possible. In deeper areas (beyond 18m) only big fragments survived. As most fragments produced by divers are small and cylindrical, consisting mainly of a broken tip, they have virtually no chances of survival (Part III, Chapter 1). Breakage by divers must therefore be considered as detrimental to the coral community, as hardly any regeneration can be expected and therefore no enhanced asexual reproduction can be expected. This situation seems to be the same in tabular species, although it has not been investigated experimentally.

The resuspension of sediment and subsequent smothering of corals may have serious consequences on a localized scale but not on a general scale. Experiments in Part III, Chapters 2 & 3 have shown the consequences sedimentation may have on both hard and soft corals. Smothering by resuspended sediment has serious physiological implications (Part III, Chapter 3), which may lead to tissue necroses if sediment levels continue to be high (Part III, Chapter 2). Coral communities adjacent to sandy areas are especially at risk. During times of high wave action natural sedimentation levels far exceed those generated by divers due to

fin-action, but much of the accumulated sediment is removed by wave-action.

e) signs of degradation

As all of the reef systems within the Marine Reserves were sampled in detail, it is possible to compare the heavily-used reefs within the Central Reef Complex with the little-used reefs in the Northern Reef Complex and the completely unused reefs in the sanctuary area in the Southern Reef Complex. The present study suggests that no serious degradation of coral communities has taken place in the Central Reef Complex. Although qualitative observations suggest a higher frequency of broken corals and a lower frequency of unattached mushroom-corals (Fungiidae), which are easily subject to poaching, it is very difficult to quantify these observations. This is due to the patchy nature of natural as well as anthropogenic disturbance in an unpolluted coral reef system. This makes it inherently very difficult to compare natural damage with human-induced damage (Rogers et al., 1988; Riegl & Velimirov, 1991) and more detailed studies are needed to confirm the present findings. It is advisable to set aside specified areas within the Central Reef Complex for continuous long-term monitoring.

f) pollution

No signs of abnormally elevated pollution levels were observed within any of the reef complexes. However, as no measurements of water-chemistry were taken it is not possible to provide conclusive information on the question of abnormally high nutrient input into the system. As increased nutrient input due to improper

sewage management can have seriously adverse effects on the health of reef coral communities (Berwick & Faeth, 1988), it would be advisable to continually monitor the situation.

The most common form of pollution found on the reefs was discarded fishing line, empty cool-drink and beer cans and floating plastic bags. At the present level this pollution cannot be considered as seriously damaging the communities, although efforts should be taken to keep pollution levels low. Plastic bags, especially, can cause damage to corals, by suffocating tissues underneath (Rogers et al., 1988). Fishing line is often found wrapped around coral colonies and can lead to breakage or, alternatively, be incorporated into the coral skeleton. It is not considered to be a major hazard at present. Empty drink-cans erode quickly and, unless present in large numbers, generally seem to interfere little with corals. They may however cause some localized physical damage in time of high water-motion, when colliding repeatedly with corals or other sessile organisms.

g) oil pollution

The grounding of the greek oil-carrier "Katina-P" in winter 1992 off Maputo (Mozambique) and the subsequent input of weathered oil clumps into the surface waters of the marine reserves was witnessed during the course of this study. Oil pollution has seriously adverse effects on the general fitness of corals, interfering with the health of their tissues, feeding mechanisms and reproductive abilities (Loya & Rinkevich, 1980; Peters et al., 1981). In the case of the "Katina-P" spill, only weathered oil-clumps and tarballs reached the Maputaland coast. The most noxious, highly evaporative and soluble substances had in all

likelihood already volatilized and the spill did not appear to cause any serious damage to South African coral communities. Although the Northern Reef Complex was not visited during the time of the spill, no obvious signs of damage were observed on the coral communities in the Central Reef Complex. As the coral communities within the marine reserves do not reach the surface, their susceptability to direct damage by surface slicks is limited. In case of an oil spill within the marine reserves, some damage can be expected, due to soluble substances in the oil reaching the corals via the water-column. Special care has to be taken to avoid even small scale spills of petrol or diesel within the marine reserves, as these substances are even more poisonous to marine life than raw-oil or bunker fuel (Clark, 1986).

The practice of washing cars and boats in the lagoon formed in the mouth of the Mgobeseleni Stream should be strongly discouraged, as this leads to input of water soluble fractions of grease, oil, petrol and diesel. In the long term, and especially at peak holiday time, when a great number of vehicles and boat engines are washed every day in the stream, this practice may lead to unacceptably high levels of hydrocarbons in the stream water emptying into the bay. This may lead to a slow degradation of animal and plant communities close to the river mouth.

h) coral bleaching

Although this phenomenon has been observed in many areas of the Indo-Pacific (Brown, 1990; Brown & Ogden, 1993, Meesters & Bak, 1993)), it has not been reported to be of any significance in South East Africa. During the present study one single incident of bleaching was observed on 4-Mile reef in an area restricted to

about $1m^2$. This should however not be taken too lightly and long-term monitoring of the coral communities is highly advisable.

f) crown of thorns and Drupella cornus

The coral-eating starfish Acanthaster planci (the infamous crown-of-thorns) and the snail Drupella cornus have been known to cause serious damage to reef coral communities all across the Indo-Pacific (Endean & Cameron, 1990; Cameron et al., 1991; Turner, 1992). No abnormally high densities of either organism were found during the present survey. It is suggested, however, that a track should be kept of the numbers of both species through a permanent monitoring program.

g) location of sanctuary areas

Two sanctuary areas, in which no human activities are permitted, are currently being enforced, one in the St.Lucia Marine Reserve and one in the Maputaland Marine Reserve (Fig. 1). Only the St. Lucia sanctuary area includes coral reefs, the two southernmost coral reefs in Africa, Red Sands Reef and Leadsman Shoal. While sanctuary areas are a very welcome feature of every reserve, several reasons would suggest a repositioning or extension of the present sanctuary areas.

The southern sanctuary area lies downstream of all other reef areas and therefore receives larval stock from the northern reefs. Due to the prevailing currents, with the Maputaland coast being swept by the southwardly flowing Agulhas current, these southern reefs have only a receiving but not a broadcasting function, as no coral communities of any importance are found further south. Due to the current, larvae originating from the southern reefs cannot

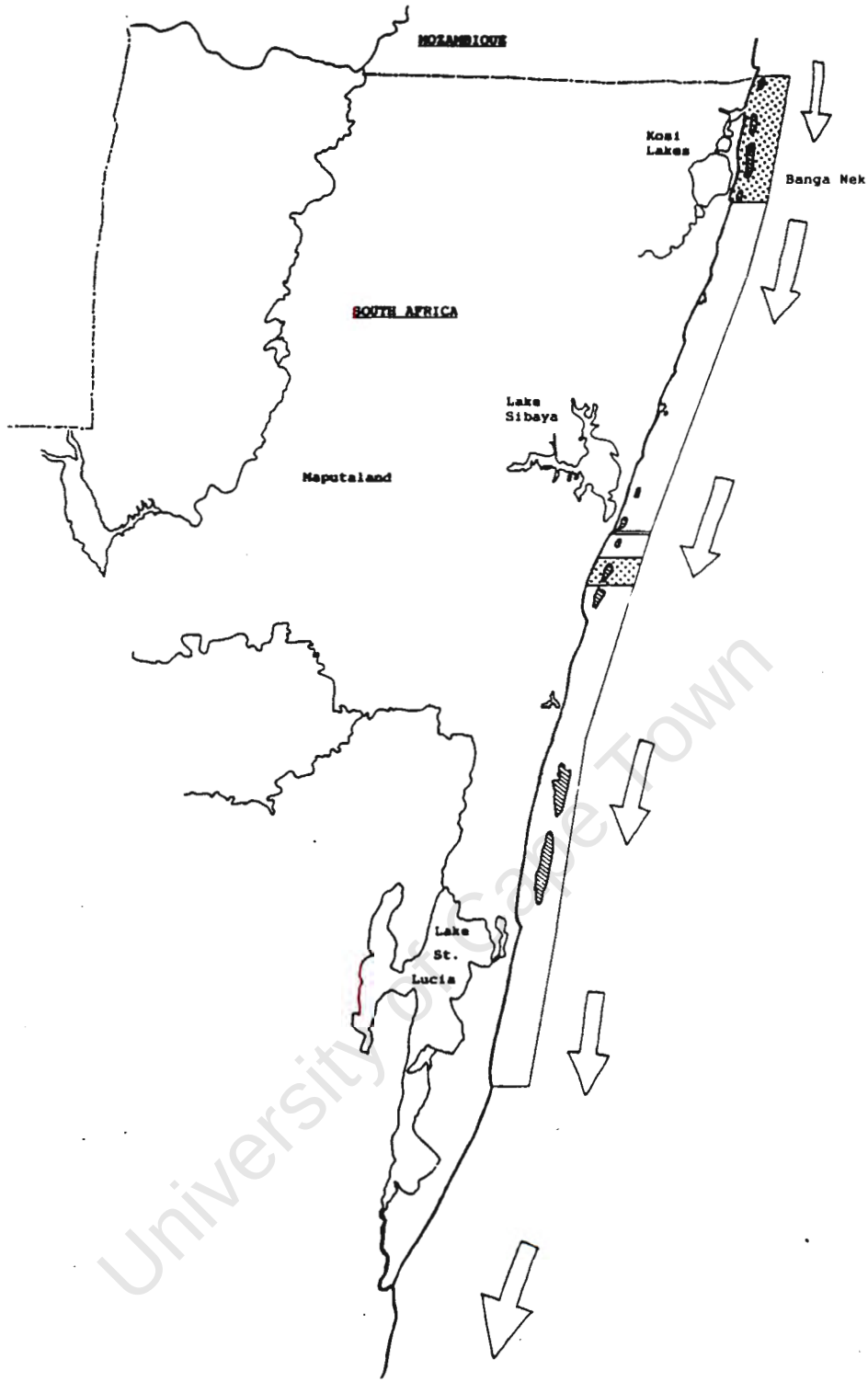


Fig. 6: Suggested sanctuary or restricted access areas (shaded) upstream of the major reef complexes in order to allow restocking of areas in case of degradation of the Central and Southern Reef Complexes. It would be ideal to have one large restocking area in the most diverse system (Northern Reef Complex, see Part II) and a smaller one in an intermediate position on the most fragile and diverse reef in the Central Reef Complex (4-Mile Reef). The dominant current direction is indicated by arrows. Community characteristics are described in detail in Part II.

reach the northern reefs. It would therefore be advantageous to position a sanctuary area as far upstream of the main body of the reef complexes as possible in order to provide an uninterrupted larval input. Ideally, this restocking area should also be positioned in the area with the highest species richness. This situation is found in the Northern Reef Complex (Part II). The upstream sanctuary would serve as a restocking area should the downstream reefs ever become depleted or degraded. The ideal position for a sanctuary would be in the Northern Reef Complex, stretching from the border with Mozambique to Banga Nek (Fig. 6). A second, smaller, sanctuary could be positioned on 4-Mile Reef in the Central Reef Complex. This reef is the most diverse in this area and I have already suggested that access to this reef should be limited due to the fragile nature of its coral communities. This second, further downstream restocking area would serve as a bridge between the Southern Reef Complex and the northern sanctuary area.

Conclusion

The present survey has not found any biologically unacceptable levels of damage or degradation of coral communities in the St.Lucia (North) and Maputaland Marine Reserves.

Three types of coral communities were identified with differential susceptability to damage. These categories are based on their structural typology as determined by the growth form of the dominant corals in the communities. The most fragile coral-community type is found on 4-Mile reef. It is suggested that diver numbers on this reef should be subject to strict regulation. Ever increasing use (Fig. 4) may lead to overutilisation of this

sensitive reef, with potentially irreparable damage. No signs of degradation were found on 2-Mile Reef, on which roughly 90% of all dives have been taking place annually. Increased use of 7-Mile and 9-Mile Reefs need not be discouraged as the coral communities there are similar to those on 2-Mile Reef and, if appropriate care is taken, no serious damage can be expected. Further information on coral communities within the marine reserves can be found in Part II.

It is further suggested that a permanent monitoring program be operated to keep track of possible changes in the coral communities.

It is suggested that the Northern Reef Complex be set aside as sanctuary area, in order to secure a guaranteed undisturbed area upstream of all other reefs. This area could then serve as reservoir of larval stock for downstream reefs.

Literature cited:

Antonius, A. 1985. Coral diseases in the Indo-Pacific: a first record. P.S.Z.N.I. Marine Ecology 6: 197-218.

Bak, R.P.M. & G.D.E. Powell. 1988. Ecological structure in a range of Indonesian fore-reef slope coral communities. Proc. 6th Int. Coral Reef Symp., Australia, Vol. 3: 191-196.

Berwick, N.L. & P.E. Faeth. 1988. Simulating the impacts of sewage disposal on coral reefs. Proc.6th Int. Coral Reef Symp., Australia, Vol. 2: 353-361.

Bradbury, R.H., Y. Loya, R.E. Reichelt & W.T. Williams. 1986. Patterns in the structural typology on two coral reefs of the central Great Barrier Reef. Coral Reefs 4: 161-167.

Brown, B.E. (ed.). 1990. Coral bleaching. Coral Reefs, Special issue 8(4): 135-232..

Brown, B.E. & J.C. Ogden. 1993. Coral bleaching. Scientific American, January 1993: 44-50.

Cameron, A.M., R. Endean & L.M. DeVantier. 1991. Predation on massive corals: are devastating outbreaks of Acanthaster planci novel events? Mar.Ecol.Progr.Ser. 75: 251-258.

Clark, R.B. 1986. Marine pollution. Oxford University Press, New York.ppl-213.

Endean, R. & A.M. Cameron. 1990. Acanthaster planci population outbreaks. in: Dubinsky, Z. (ed.): Coral Reefs-Ecosystems of the world 25; Elsevier, Amsterdam-New York: 419-437.

Jaap, W.C., J.C. Halas & R.G. Muller. 1988. Community dynamics of stony corals (Milleporina and Scleractinia) at Key Largo National Marine Sanctuary, Florida, during 1981-1986. Proc.6th Int. Coral Reef Symp. Australia, Vol.2: 237-243.

Loya, Y. 1978. Plotless and transect methods. in: Stoddart, D.R. & R.E. Johannes (eds.): Coral reefs- research methods. UNESCO Paris: 581-591.

Loya, Y. & B. Rinkevich. 1980. Effects of oil pollution on coral reef communities. Mar.Ecol.Progr.Ser., 3: 167-180.

Meesters E.H. & R.H. Bak. 1993. Effects of coral bleaching on tissue regeneration potential and colony survival. Mar. Ecol. Progr. Ser. 96: 189-198.

Peters, E.C., P.A. Meyers, P.P. Yevich & N.J. Blake. 1981. Bioaccumulation and histopathological effects of oil on a stony coral. Mar.Pollution Bull. 12(10): 333-339.

Porter, J.W & O.W. Meier. 1992. Quantification of loss and change in Floridian reef coral populations. Amer.Zool.32: 625-640.

Ramsey, P.J. & T.R. Mason. 1990. Development of a type zoning model for Zululand coral reefs, Sodwana Bay, South Africa. J.Coastal Res. 6(4): 829-852.

Ramsey, P.J. 1991. Sedimentology, coral reef zonation and late pleistocene coastline models of the Sodwana Bay continental shelf, Northern Zululand. Unpubl. PhD thesis, University of Natal, pp. 1-202.

Riegl, B. & B. Velimirov. 1991. How many damaged corals in Red Sea reef systems? A quantitative survey. Hydrobiologia 216/217: 249-256.

Rogers, C.S., L. McLain & E. Zullo. 1988. Damage to coral reefs in Virgin Island National Park and Biosphere Reserve from recreational activities. Proc. 6th Int. Coral Reef Symposium, Australia, Vol.2: 405-410.

Talge, H.K. 1991. Impact of recreational divers on scleractinian corals of the Florida Keys. MSc Thesis, University of South Florida: 1-92.

Turner, S. (ed.). 1992. Drupella cornus: a synopsis. CALM Occasional Paper No. 3: 1-104.

Wainwright, S.A., W.D. Biggs, J.D. Currey, J.M. Gosline. 1976. Mechanical design in organisms. Princeton University Press. pp.1-423.